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ON THE DISPERSAL OF THE PLANTS MOST INTIMATE TO BUDDHISM

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A FAITH that forbad digging was ill-equipped to advance horticulture: such was primitive Buddhism. But from among plants which were already dear in cultivation it took a few for its own venerations and exercised an influence in their dispersal. It is with these few that this paper deals. As the subject is near the extreme bounds of horticulture it is well at the outset to remind the reader when and where the possible influence on horticulture by Buddhism originated.

The religious philosopher and founder of Buddhism, Siddhattha, son of a Sakya prince and Māyā, one of the prince's two wives, called from his parentage Sakyamuni or the recluse of the Sakyas, of the clan Gotama (Pali) or Gautama (Sanskrit), enlightened teacher and therefore called buddha, was born about the year 567 B. C. Of the several ways of naming him, the best is by his clan as he would have been addressed in life; he is the Buddha Gautama and when so named cannot be confused with the many hypothetical buddhas of the religion. By that name I shall call him. In his late twenties, as the Pali text expresses it, "going from house to houselessness," he crossed the Gangetic plains from his birthplace under the Himalaya of Nepal to Rājagaha, now Rājgir, where low hills rise that have become honeycombed with hermit cells; then he moved a little farther south to the place now known as Bōdh Gayā, and there, after eight years of meditation, an understanding came to him as he sat in the shade of a tree of *Ficus religiosa*. The assumed date is 528 B. C. Thenceforward he was a missioner crossing and recrossing the plains between Rājagaha and the Himalaya until his death in old age about 487 B. C. (cf. for the establishment of these dates, Vincent Smith, Early Hist. Ind., ed. 4, p. 49, 1924, or other editions). The whole of his preaching had been within the limits of the two kingdoms of Kosala and Magadha, say between the longitude of Lucknow and the breaking up of the Ganges into its delta; and all the plants that the faith associated with him should have been familiar within that area at that time.

The language in use was Pali, which was superseding Vedic, to be superseded itself later by Sanskrit. The upper Gangetic plains were completely aryanized; but where Gautama preached the aryanization was incomplete. It is obvious that the pre-aryan population possessed a considerable agriculture, but of its nature we know nothing save that it cannot have been despicable. Indirect evidence suggests that the land enjoyed a prosperity which aided Gautama in withdrawing from Brahmanism a sect of itinerant missioners entirely dependent on what the land had to spare. These missioners, when the annual Rainy Season immobilized them, as the oldest rules of the Faith show that it did, gathered in groups to edify and teach each other; and in that way they handed down by word of mouth the whole of their beliefs, the philosophy behind them, and the sermons supporting them. They continued to do so until an off-shoot priesthood in far-away Ceylon, in fear that the human chain would be broken, in troublous times in the 3rd century B. C., began piously to commit to palm-leaf books their vast memorized store. Ecstatic minds had spread unevenly over the kernel an inevitable incrustation; and the incredible in the records casts a shadow of suspicion that the background on which one would like to rely may be the background of the time of writing rather than the background of Gautama's day. The Buddhist monuments do not help, for they belong more or less to the time of the writing and are therefore suspect in the same way. Some little light comes from Brahmanistic literature.

Of all plants the Sacred Lotus, *Nelumbium Nelumbo* (L.) Druce, entered deepest into the religion; and it seems good to consider it first. Lotus it should not be called, but Sacred Lotus. This beautiful water-lily grows naturally in a belt across Asia from the delta of the Volga to Japan and, southwards of the belt, through India, China, the Indo-Chinese countries, and Malaysia to New Guinea and northern Australia. It requires still water, the temperature of which rises in summer to 80–95° F.; winter temperatures which freeze the water above it do not hurt it. In fact it is benefited by contrasted seasons. It is intensely light-hungry and therefore shaded waters do not support it, with the consequence that it is absent from wide stretches of the moister tropics, just as it is absent from wide stretches of mountains where there is no still water for it. Man, when he digs hollows for storing water, creates places which may be favourable, but are not necessarily so if the plant cannot get food enough in them. Its several limitations cause its natural distribution to be patchy, but leave it easy to cultivate.

The Aryans must have known it before they pressed south and east, round the mountains of Afghanistan into the Indus plains. This was before 2000 B. C. Their worship included Sun-worship and they seem to have linked *Nelumbium* with sun-rise, just as the Egyptians linked the blue water-lily of their swamps. But the Aryans' dawn-flower was rose-pink like the dawn-flower of the Greeks. *Nelumbium* possesses several

appropriate characters in addition to the suggestiveness of its colour; it opens, often very abruptly, at dawn, and like the Egyptian Water-lily it possesses that property most naturally important in Sun-worship of rising into the air from a void of waters. Moreover it is very beautiful: cannot dawn be very beautiful in clear more or less desert skies!

The reason for holding that the Aryans gave the Sacred Lotus a place in their Sun-worship is that their descendants, when they had settled in India and their priestly observances came to be recorded in the Rigveda, showed that they kept the connection, making the flower the eye of a personified Sun and garlanding with it certain horsemen, the Asvins, sons of the Sun, betrothed to the personified Dawn. The connection with the birth of the Day passed into making its pretty cup a birthplace in general, — for the beautiful goddess Lakshmi in Brahmanism and for all good occasions in Buddhism; and today fairies are born in the flowers in the folk tales of more than one country in the East.

The Vedic name "pushkara," which is used in the Rigveda, has a connection by its meaning with the edibility of the rhizome. It yielded place to the Pali "padma"; it is questionable why, but it may have been that the utility expressed in the word "pushkara" brought it about, just as in German "See-rose" has displaced the old High German "Kolerwurtze"; — this is utility displaced by the aesthetic. Furthermore it may be added that in Sanskrit the word "padmaka" appeared by the side of "padma" as a name for the rhizome, having the meaning of "belonging to padma," i. e. the rhizome was put in second place.

At the time of Gautama it cannot have been otherwise than that his compatriots, ready enough to eat the rhizomes and seeds and to use the leaves as platters, loved the plant very particularly for its beautiful flowers. It was honorific to present all pretty flowers in homage but especially its flowers, to seat a ruler on a seat carved as the flower (a "padmasana"), and to place august feet on a stool similarly carved. There is a parable in the Jatakas or Birth stories of Buddha (Jātaka no. 261) indicating that it was cultivated to meet a trade in flowers so established as to feed a flower-bazaar; and as this parable introduces the name of Ananda, Gautama's cousin and most faithful disciple, the existence of the trade is claimed for the time of Gautama. It is evident that they who wrote down the story, and dated it thus 300 years or so before the time of their writing, thought there was no anachronism in attributing the trade in the flowers to that time.

The use the followers of Gautama made of the flowers as an honorific was at first that which others who were not his followers made of it. It was a social custom.

In the year 1898, a planter and skilful surveyor, William Claxton Peppé, carefully opened a reliquary mound at the village of Piprāhwā in the Basti District of northern India, close under the Himalaya of Nepal. He unearthed among other deposits a beautifully shaped steatite vase containing undoubted relics of Gautama, and inscribed as the pious foundation

of the Sakya brethren with their sisters, children, and wives. The inscription is held to be of the time of the great buddhist emperor, Asoka, suzerain of three-quarters of India from 272 to about 232 B. C.; and therefore there had been a reburial, so that the date of flowers in gold and silver deposited with the relics is to be taken rather as 247 B. C., which is when Asoka made his recorded pilgrimage to the holy places of his faith, than as near 487 B. C., when Gautama died. That this is right two further considerations suggest, namely (a) with the flowers are trisulas and other emblems likely to have been accretionary in the religion after Gautama's death, and (b) similar flowers have been found in monuments of about Asoka's time. Thus the evidence the deposited flowers afford is to be dated 2½ centuries after Gautama's death. The flowers and other associated objects were drawn, as found, by Mrs. Peppé, and her drawings were reproduced on a plate inserted into the *Journal of the Royal Asiatic Society* (1898, opposite p. 579). Peppé, on p. 576, describes them as "ornaments in gold, gold beads, impression of a woman's figure . . . svastika . . . and quantities of stars or flowers both in silver and gold with six or eight petals each." With the identifications of these two kinds of flowers I am immediately concerned, and in the first place with the six-petalled. They may have the petals rounded or pointed, and if rounded they are very well described as like Forget-me-not flowers with one petal too many. Of Indian flowers they exactly resemble those of the Teak tree. But surely Gautama never saw a Teak tree, as he spent his life to the northward of the area in India which the Teak occupies; and his followers had no reason to connect that tree with him. These flowers in precious metals I determine as conventional representations of Sacred Lotus flowers. As to the improbability of their origin being the Teak tree, Watters' association of this tree (which was in Sanskrit called "Sāka") with the Sakya tribe whence Gautama came (Jour. Roy. As. Soc., 1898, p. 570) sent me hunting for myths that might have led to a connection, but altogether without success.

I have mentioned that the flowers in the Piprāhwā find were illustrated from drawings; a similar find of flowers in gold and silver was made at a village called Bhattiprolu in the Kistna District of the Madras Presidency and was illustrated photographically by Alexander Rea in volume 15 of the *Reports of the Archaeological Survey of India* (1894, *pl. 1*). Three vases were found and their contents are shown on this plate; in the first vase were relatively large eight-petalled flowers, along with smaller six-petalled flowers and a few five-petalled; in the second vase were 164 flowers, two-thirds of them six-petalled, most of the rest eight-petalled, and just a few five-petalled; in the third vase with one exception all the flowers were six-petalled. The reader will note that the eight-petalled flowers are as a rule larger than the others; they must have cost more in the market.

Fully 800 miles separate Bhattiprolu from Piprāhwā.

The image of the six-petalled flower is found cut into the stone in the

buddhist monuments of Bōdh Gayā, Bharhut, and Sānchi, which stand wide apart across the centre of India. The representations are so alike that if one is accepted as the flower of the Sacred Lotus, all must be; therefore the distribution of the conventional emblem was wide, fully as wide in any direction as the distance of Bhattiprolu from Piprāhwā suggests. At the Bharhut Stupa the flowers are scattered over altars and are mixed with representations of Sacred Lotus flowers in side view which are not conventional at all nor deceptive (for illustrations of them see Sir Alexander Cunningham's "Stupa of Bharhut," 1879, *plates 13, 14, 15, 17,* and *29*). At Bōdh Gayā the flower is represented on a panel as covering a tree; the tree is fenced round, and the fence serves as an identification mark showing that the tree was the sacred bodhi tree under which Gautama attained enlightenment, his *Ficus religiosa*; therefore the flowers are not its own, but honorific Sacred Lotus flowers put over it as garlandings (see Rajendralala Mitra's "Buddha Gaya," 1878, *plate 38*). The same flower fills niches in the design of one of the gates at Sānchi (see Maisey's "Sanchi and its Remains," 1892, *plate xii* and cf. *plate xxvi*; also Foucher and Marshall, "The Monuments of Sanchi," *plate 51b*).

I have given references enough to show how firmly this conventional representation of the flower must have been established, and I feel assured that the reader will consent that the Bharhut and Bōdh Gayā carvings determine what that flower is.

The eight-petalled flower admits of no mistaking. The natural flower is enclosed in four sepals, and petals follow to an uncertain number; the representation of a flower, should it realistically start with four to indicate the sepals, naturally proceeds with another four and thus eight is reached. The followers of Gautama in time connected the number eight in this flower with "the Noble Eightfold Path" from conversion to enlightenment. The simile did not lead to the device, but the device to the simile.

The flower in gold with five petals, which is present in small numbers in the finds, must also have represented the Sacred Lotus, partly on the argument that the departure from realism by which the six-petalled flower was reached was easy of extension to five, and particularly that five-petalled flowers terminate the arms of composite ornaments made up of six-petalled flowers, being set at the ends as smaller.

From the eight-petalled representation of the flower, Buddhist carving, statuary, and pictures increased the number of petals according to available space, usually by four at a time.

The early Buddhists claimed that Gautama on his death-bed had enjoined four pilgrimages. Whether he did or did not is immaterial, seeing that the pilgrimages came into being. The first was to Kopilavastu, near which he was born, and its symbol was the Sacred Lotus flower; the second to Bōdh Gayā, where he obtained enlightenment, and its symbol was the sanctified *Ficus religiosa* under which it occurred; the third to Benares, where he preached his first sermon, and its symbol was the wheel; and the

last to Kusinagara, where he died, and its symbol was a funeral mound (see Foucher in Mem. no. 46, Archaeolog. Survey India, 1934). Though the Sacred Lotus belonged in the greatest measure to Kopilavastu, it is clear that it conveyed to the Buddhists ideas so essential as to be an emblem everywhere; and it is evident that pilgrims offered the flowers not only at Kopilavastu but at the shrines generally, not merely the natural flowers which were more often out of season than in season, but gold and silver representations of them as an alternative or an accompaniment.

Why enshrine the gift in this form? Firstly, it was not coin which the brethren were forbidden to accept, although they did when lax. Secondly, the choice of the flower in gold as a means of honouring was established before Gautama's day. For instance, in the Vedic Satapatha Brāhmana it is directed that a king at his coronation should be garlanded with "pushkara"; and in the later, but still Vedic, Sayana and Katyayana it is suggested that the flowers be of gold and the ceremonies protracted over a whole year, i. e. over months when the natural flower could by no means be procured. Naturally, then, the buddhist priesthood valued the combination of honour and alms that the flowers in gold or silver brought to the altars. And this having been stated, the reader will understand why I have been anxious to make the point that five-petalled, six-petalled, and eight-petalled emblems do not represent rival flowers, but the one only, offered in different sizes. The pilgrim who placed his offering on the altar would of necessity take the smaller flower should his purse be too small to admit of the larger, and the artisans who made the flowers, cramped by the need of getting the price down to meet exhausted pockets, seem to have decided that a reduction to six petals brought the cost down without destroying the similitude of the emblem. I see no reason for seeking another explanation and am fully satisfied that the six-petalled and the eight-petalled are not rivals for honour.

The Sacred Tooth at the Temple in Kandy is placed, when on exhibit, in a golden Sacred Lotus flower.

There are so many figures in buddhist sculpture of flowers in vases that we know they were thus placed on altars. Otherwise in ceremonials they were strewn about.

The buddhist monasteries from very early times made fish-ponds in their grounds, not that they might eat the fish, but that the keeping of the fish might be an act of charity. *Nelumbium* likes plenty of manure; the fish provided it; the plants throve and the altars were well supplied with their flowers. It would be an object to raise freely flowering plants, and, as scent was desired, to choose well scented races; but outside the monasteries greater selection was probable from the luxury of sprinkling the flowers over beds, a luxury expressly forbidden to the priesthood. At times white-flowered races met with favour and were assigned as recognition marks to certain saints. It happens that today the strongest scented flowers in European markets are those of a white-flowered race.

When Buddhism travelled beyond the boundaries of India, it carried the name "padma" as an ecclesiastic name to countries where the plant had its established secular name; and so it is that "padma" or "padema" is known in Ceylon beside "nelun," "nelum," and "nelumbu"; in Burma beside "kya"; in Siam beside "bua"; and in Java beside "tarate." Sometimes the secular name, because it covers species of *Nymphaea* as well as *Nelumbium*, needs for precision a distinguishing adjective.

In China the plant has more than one name, which in an interesting way indicate different parts of it. The chief name is "lien"; it is not ecclesiatic, though "pai lien" or "precious lien" is the Sacred Lotus flower held in the hand of the image of Kuan Yin, the divine source of infinite mercy.

Attention may be drawn in passing to what is apparently an ecclesiatic name used in the northern Shan States, where "poh bo" (that is, "bo" flower, apparently for "poh bo-da" or Buddha's flower) is met with in Palaung (see Mrs. Milne's Palaung-English Dictionary, p. 31).

Nelumbium blossoms in northern India in the months of August, September, and October, after which the buddhist altars would be bare of it. Certain Sanskrit names point to substitutes, chief of all to *Hibiscus mutabilis* Linn., which was called "sthala padma" or "land padma." This name persists in use in Bengal in the form "thalpadma." At the same time this pretty flower was "padmavati" and "padma carini" meaning "like padma." It may be assumed that, as a shrub which could be grown in monastery parks, it had its place, and that its pink flowers served as a substitute.

In Monier-Williams' Sanskrit Dictionary two other plants are said to bear the name "padma." He quotes both from Indian lexicons and therefore the dates of their use are not indicated. The first is the dye-plant *Carthamus tinctorius* Linn.; but it would not be a substitute. Its association arose in the colour which it dyes. The other is *Clerodendron siphonanthus* R. Br., more properly named *C. indicum* Kuntze; and here I suspect an error in identification, for *C. siphonanthus* has not the resemblance to the Sacred Lotus which *C. fragrans* Vent. and in a less measure *C. infortunatum* Gaertn. possess. It would seem reasonable to transfer employment at the altar to these two, but not to the first.

The Chinese associate *Hibiscus mutabilis* with Confucius, calling it "fu jong," a name which extends into Cochin-China and Siam as "fu yong." On the other hand the Chinese give the name "fo sang" or Buddha's mulberry to *Hibiscus rosa-sinensis* Linn. The ideograms for "fu" and "fo" are very unlike; but because of the similarity in modern pronunciation it seems right to ask that some sinologue look into the application of the two names.

India, today, regards the "tulsi," *Ocimum sanctum* Linn., with more affectionate veneration than any other plant, giving the second place to *Ficus religiosa* Linn. Buddhists put the latter into the forefront of their faith because Gautama attained enlightenment when, as already stated,

meditating under a tree of this species — his bodhi tree: they gave no place to the *Ocimum*. There is a reason for the Indian villager's preference which is not religious; he can and does grow the *Ocimum* at his house door, but as a rule it is out of the question for him to seek space for a tree so umbrageous as the *Ficus*; it is better to let the village have a communal tree, and so it is arranged. There is also a reason for the Buddhist's disregard of *Ocimum*: namely that the faith forbad digging, and *Ocimum*, by demanding a clean-weeded square foot of soil, asks for it. But to take a small branch of the *Ficus* and to thrust it into the soil as a cutting broke no regulation; and it grows.

The reader will observe in reading this paper that with the exception of *Nelumbium*, all the plants named as intimates are woody: they were all suitable for positions in parks, growing in them without particular attention. Moreover, he will note that *Nelumbium* was raised assuredly without any turning over of soil for it. *Ficus religiosa* readily obtained a place in such parks, and, if by a cutting taken from Gautama's own bodhi tree, so much the more valuable the scion raised. From the founder's tree, according to Jātaka no. 479, a cutting was taken with Gautama's consent to Jetavana in Savatti and planted at one of the town's gates; and it is recorded also that in the 3rd century B. C. the park of Mahamegha, near Anuradhapura in Ceylon, acquired a cutting, and that other cuttings followed until Ceylon had eight. The name "bodhi druma" or tree of enlightenment could scarcely become a distributed vernacular name for this fig until such events began to take place, for it indicated at first an individual tree.

Ficus religiosa is native in the foot-hills of the Himalaya from the Punjab eastward, and of moist country southward as far as the borders of the Madras Presidency, and it is native through Burma almost to Rangoon. Nature spreads it by very minute seeds; and the minute seedling must have plenty of light and moisture. These two needs, acting together, produce restricted limits; but Man can take cuttings, and as the tree is very tolerant of climate when once established, can spread it widely. It is grown from cuttings even in a country so dry as Beluchistan (see the writer's "Working List of the Flowering Plants of Beluchistan," p. 70, 1909). If it be right, and it probably is right, that the Aryans were struggling for lands in the Indus plains when the great town of Mohenjo-daro existed, say in about 2000 B. C., they would have met with the tree on entering India, for Sir John Marshall identifies it with a fair measure of certainty on a seal found there ("Mohenjo-daro and the Indus Civilization," 2, p. 390, 1931). The tree tolerates the climatic conditions of today in the Indus delta (cf. Blatter and Sabnis, "Flora Indus Delta," p. 29, 1929), and there is nothing unreasonable in thinking it could have been carried that far by cuttings. Male plants of *Salix tetrasperma* Roxb. show by their dispersal in southeastern Asia how readily a plant may travel by cuttings.

The *Ficus* is widely seen on roadsides, giving grateful shade; and the Aryans would appreciate this usefulness as well as its yield of fodder. There are, of course, no written records of it at very early dates; but its name "pippala" is met with in the late Vedic Brhadāranyaka Upanishad in a way which MacDonnell and Keith (Vedic Index, 1, p. 531, 1912) regard as a reference to the tree.

The tree marks mid-winter by shedding its leaves and standing bare for a strikingly brief period of two or three days: this and the restlessness of its leaves in any light breeze make it mystic enough to seem a possessor of secrets. Consequently it was prayed to in the Vedic Atharvaveda, and up to our times the Indian villager, especially he of the south, places in its shade the prayer for offspring that he makes when he dedicates a snake stone.

The selection of a seat under it for Gautama's meditation would not be altogether fortuitous.

As the time of its leaf-fall coincides with the anniversary of Gautama's death, the Buddhists decided that it has memorized the event.

Ficus religiosa, of extended dispersal already when Gautama was born, invited buddhist aid for faster travel; and good proof that such aid was given is obtained by the distribution of names derived from the Sanskrit "bodhi druma" or tree of enlightenment. There is "bo gaha" or bo tree in Ceylon; "nyaung bo de" in Burma where "nyaung" is applied to a group of large figs; "cay bodi," "cay budde," and "cay de" in Annam; "bu" or "but" in the Cham language; "po ton" or po tree in Siamese; "d'om p'o" in the Khmer language; "kayu bodi" or bodhi tree in various parts of Malaysia; "p'u t'i shu" or bodhi tree in Chinese; and "bodai ju" in Japanese. But the names are sometimes applied to *Ficus Rumphii* Blume, and sometimes to species of *Tilia*, notably to *T. Miqueliana* Maxim. The two misapplications are of very different degree, for *Ficus Rumphii* is so similar to *F. religiosa* that its appearance justifies the transfer of the name, and in Annam and Malaysia the demand for *F. religiosa* about shrines may be met by *F. Rumphii* in a way which arrests the dispersal of *F. religiosa*. But no similarity justifies the transfer of the name to *Tilia*, which northern Chinese and Japanese, being unable to get the *Ficus* to grow in their climate, made in a kind of desperation. Its interest is chiefly in demonstrating the intensity of a demand that could produce such an unreasoned substitution. Modern Japanese botanical works record the name "bodai ju" as indicating *Ficus religiosa* as well as four or five different species of *Tilia*, most of them favourite trees in their country, with highly scented flowers, and frequently planted.

It was stated at the outset of this paper that Gautama's mother was named Māyā. She, expectant of the birth of her child and wishing it should take place at Devadaha, was travelling thither by palanquin from Kopilavastu and had reached a grove of trees half way when overtaken by labour. Some call the place the Lumbini Garden; but the word garden

implies cultivation, whereas the biographic commentary Nidanakatha calls it a wood of variegated climbers, a mass of flowers and fruits, and in it a mighty "sāla" tree. In this grove Gautama was born, his mother clutching a branch of the mighty tree.

"Sāla" is the Pali and Sanskrit name of *Shorea robusta* Gaertn., and shortened to "sāl" persists in Hindi and Bengali. Of the continuity of the application of the name there is not the slightest doubt, particularly as "sāla" was the principal building timber of northeastern India in those days, when all buildings were of wood, and it was in such great use that "sāla" also meant a house. There is an interesting story in the Jatakas (no. 465) of the choice of a great tree for the making of a palace.

As Māyā's journey would bring her among "sāla" trees the story has no geographic incompatibility; but as trees when well grown carry their branches far out of reach, the story had a difficulty to circumvent which it did by making the branch bend miraculously to Māyā's hand.

Gautama's association with the "sāla" did not, however, end with this, for on his last mission he died, lying on his cloak, which Ananda folded and placed for him on the ground between two "sāla" trees; and this solemn event gave a sanctity to the species greater than that of his birth, one which made devout Buddhists anxious to grow the tree about their establishments. But it must have proved intractable. The tree drops its seeds in winged fruits at ripeness and they germinate at once; if they be foiled they die. Foresters in India complain that a layer of dead leaves on the soil is enough to frustrate establishment, as the seed dies while it is delayed in getting anchorage. Its quick death made transport by seed of no avail.

It is remotely possible that Kashmir monasteries, in their inability to raise *Shorea*, substituted *Aesculus indica* Hiern, an Indian Horse Chestnut; but that is not demonstrated. The Chinese, whose pilgrims were certainly familiar with Kashmir, for some unexplained reason took their *Aesculus chinensis* Bunge, which is very like *A. indica*, for "sāla," calling it "so lo" and planting it about their monasteries. There is otherwise no reason for thinking that the Kashmir Buddhists may have taken their tree for the "sāla"; though it would have been, as today, a favourite for planting. No one has as yet found a vernacular name applied to it which could be derived from "sāla." Alternatively the acceptance of *Aesculus chinensis* may have had no more behind it than the acceptance of the *Tiliae* already mentioned.

The flower of *Shorea robusta*, cut in gold leaf, was present in the Piprāhwā find.

When in 249 B. C. the great buddhist emperor, Asoka, went on pilgrimage to the holy places of his religion and came near Kopilavastu, his spiritual preceptor, Upagupta, arrested him with the words, "Here, Great King, was the venerable one born." Asoka marked the spot, but the tree grasped by Māyā, according to the records of Asoka's visit, instead of being

Shorea robusta, was that known today through northern India and yet more widely by the very name of the emperor himself — the "asoka," *Saraca indica* Linn., its sanskrit name meaning without sorrow. It is a small tree, branching low, so that Māyā would have had no difficulty in grasping it. When it flowers it is of great beauty, the flowers being from a pale citron to a ruddy orange, and deliciously scented. The poetry of introducing into the story a plant with a name of such meaning and the flattery of doing so in the reign of a ruler of the same name are obvious. Worthiness was preserved: if Māyā's contact was not to be with the greatest tree, it might well be with the most beautiful available flower. There was no geographic incompatibility; for *Saraca indica* is proved to grow by streams in the foothills of that part of the Himalaya. Thence it spreads eastward toward southwestern China and southward in the moister mountains of Peninsular India to Ceylon. It is also in Tenasserim. It is a great garden favourite in parts of India near its natural habitats.

The word "asoka" may have recalled to the reader's mind an English poetic name of the same meaning — "hearts-ease." Names like this are of small valency: they may slide off; and "hearts-ease" did so, for in the sixteenth century it was used for the Wallflower, *Cheiranthus Cheiri* Linn., as well as for the Pansy, *Viola tricolor* Linn., and then slid away from the Wallflower. Similarly "asoka" was not so firmly attached as it is now to the one plant, but denoted also scarlet-flowered species of the genus *Ixora* and apparently other pleasing plants. I have mentioned resort at the altar to *Hibiscus mutabilis* when *Nelumbium* was out of flower; so resort would seem to have been made to *Ixora coccinea* Linn. when *Saraca indica*, after a rather short flowering in the Hot Weather, went into seed; the *Ixora*, whose flowering is very extended, then comes to its best and continues so through the Rainy Season. Prain (Bengal plants, p. 571, 1903) has suggested Chittagong to be the home of this plant. It would seem to have been joined early in Indian gardens by *Ixora stricta* Roxb., from a little further to the east.

To the south of the Vindhya hills "asok" is applied today to the umbrageous tree *Polyalthia longifolia* Benth. & Hook. f., which is unlike *Saraca* and *Ixora* in every respect save that it is cultivated; and Tamils call it "assothi" which is the same name. It is a native of Ceylon and has been brought northward as far as the Gangetic plains by Man's plantings.

There is a curious use of the name "asoka" by the great Chinese pilgrim Hsuan-tsang. He narrates that he was set on by robbers a short distance down stream from Ayudhia in a wood of "asoka" trees (Julien, Hist. Vie de Hiouen-thsang, p. 116, 1853; Watters, On Yuan Chwang, 1, p. 360, 1904; and Beal, Life of Hiuen-tsiang, p. 86, 1911: Julien transliterates the word 'o-chou-kia). I refer to this because it is incredible that *Saraca indica* could have existed as a wood on the sides of a navigable river out in the plains; and Hsuan-tsang could not have meant *Saraca*; nor could

he have meant *Polyalthia longifolia.* It is impossible to state what he meant; but the use of the word suggests that to him at least "asoka" was not necessarily *Saraca.*

If "asoka" has been thus loosely applied, it is necessary to take up with the scholars their interpretation of "asoka" in such writings as the Vedic Brihat Samhitā. But Bana, who wrote rather more than a century after Hsuan-tsang had left India, very definitely knew *Saraca indica* as "asoka" and *Ixora coccinea* as "bandhuka."

That the name "asoka" originated in the plains of northern India is certain; it travelled southwards, keeping its form; but across the Bay of Bengal it lost its initial letter, appearing in the Siamese language as "sok" and in the Sundanese as "soka," which are in Siam and Java, respectively, applied to *Ixora.* It is quaint that those who use the name deprived of its first letter go about unknowingly calling it sorrow. In Tenasserim the beautiful *Amherstia nobilis* Wall. has the name "so-ka," apparently of the same origin. Kurz, who first recorded it, does not extend this spelling to *Saraca;* but he makes *Amherstia* and *Saraca* share the name as "thauh-ka." I have improved his transliteration.

The Chinese have translated "asoka" into "wu yu shu" or no sorrow tree.

Whether a four-petalled flower cut into the stone carving at Bharhut be *Saraca* or *Ixora* is impossible to state, but it is probably either the one or the other (for illustration see Rajendralala Mitra's Buddha Gaya, *plate 32*); but the four-petalled flower in the hand of the figure of Gautama and that in the hand of the figure of Padmapani are certainly intended to be *Nelumbium.*

Shorea robusta and *Saraca indica* were not, however, the only trees said to have been grasped by Māyā; in the Lalitavistara, a Buddha epic of the commencement of our era, she is made to grasp a branch of *Ficus religiosa.* This substitution is late and had its obvious origin in the Indian belief that the foot of this tree is definitely connected with offspring. Then again there is a version of her conception which makes her to be taking a siesta under one of these trees when she dreams the dream which interpreters of dreams explained as marking the moment when she conceived. In other versions her siesta was in the palace.

Watters (On Yuan Chwang, 2, p. 16, 1905) calls attention to a Chinese translation of the Lalitavistara in which Māyā is made to grasp a branch of the "lin-pi" tree. This is not a claim for yet another tree; but "lin-pi" = "lumbi," as he explains, must mean no more than the tree of the Lumbini Grove.

The identical tree which Māyā grasped, the tree which Asoka saw, is said to have been seen in a dying state in A. D. 400 by the pilgrim Fa-hien, and in a dead state over 200 years later by Hsuan-tsang. Now a tree of *Shorea,* if a giant in 567 B. C., had surely died long before A. D. 400, and a tree of *Saraca* had certainly died. Substitutions may have occurred,

just as in the case of the *Ficus* at Bōdh Gayā, which substitutions the reader will find recorded by Rajendralala Mitra in his book "Buddha Gaya."

Imaginative disciples during the most accretive years of Buddhism assigned various pleasant trees to hypothetical buddhas, that they might be described as obtaining enlightenment under them or as doing various acts under them. Such trees were *Melia indica* Brandis, *Michelia Champaca* Linn., *Mesua ferrea* Linn., *Terminalia tomentosa* W. & A., *Albizzia Lebbek* Benth., etc. To collect together their names would seem to be a way of knowing what was to be found in the monastery parks; but there were princely courts that laid out parks of the same nature, and the priest did not promote the dispersal of these trees more than the prince, sometimes perhaps less than the prince.

My study of the few that were really intimates began with the collecting of sanskritic names current in Indo-Chinese and Malaysian languages in a wish to know how certain plants of India had come to travel. *Nelumbium* had not needed transport, but obtained from Buddhists some increase in abundance; *Ficus religiosa* had its range extended, but was not always preferred to *Ficus Rumphii*; *Shorea robusta* resisted being taken out of its natural area; *Saraca indica* and *Ixora coccinea* were taken across the Bay of Bengal, not necessarily by Buddhists but by those who laid out parks, whether Buddhists or not. All the trees named, unless the *Terminalia* be excluded, had a definite horticultural value and by that value they are still progressing eastward. Dr. E. D. Merrill indicates, in his "Enumeration of Philippine Flowering Plants," the relatively recent arrival of most of them at the farther end of Malaysia.

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THE CLASSIFICATION OF MALAYAN BAMBOOS

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IN STUDYING the bamboos of the Malay Peninsula, with the help of Gamble's great work (4), I found some difficulty in distinguishing between the genera *Gigantochloa* and *Oxytenanthera*, and I was struck by the resemblance in spikelet-structure between these genera and *Dendrocalamus*, though the latter is placed by Gamble in a different subtribe. This led to a consideration of the basis of Gamble's classification (little modified from the earlier one of Munro), namely fruit-structure, in which again I found agreement between *Gigantochloa* and *Dendrocalamus*; I also found that neither genus differed greatly from *Bambusa* in the gross structure of the fruit. A re-arrangement of Gamble's scheme therefore seemed necessary and was attempted. The result is given below, after discussion of the factors involved. It needs checking by examination of other species, and completing by examining the flowers of *Dinochloa* and the fruits of *Schizostachyum* and *Ochlandra*. I hope however that the scheme, though incomplete, will help others who may have the opportunity of examining bamboo flowers and fruits.

For the sake of convenience, I give here Gamble's conspectus of the subtribes of Indian bamboos:

1. ARUNDINARIEAE (none Malayan).
2. EUBAMBUSEAE. Stamens 6. Palea usually 2-keeled. Pericarp thin, adnate to the seed.
   Genera: *Bambusa, Thyrsostachys, Gigantochloa, Oxytenanthera.*
3. DENDROCALAMEAE. Stamens 6. Palea 2-keeled. Pericarp fleshy or crustaceous, separable from the seed.
   Genera: *Dendrocalamus, Melocalamus, Pseudostachyum, Teinostachyum, Cephalostachyum.*
4. MELOCANNEAE. Stamens 6 or more. Spikelets 1-flowered. Palea more or less similar to the flowering glumes. Pericarp crustaceous or fleshy, separable from the seed.
   Genera: *Dinochloa, Schizostachyum, Melocanna, Ochlandra.*

Fruits of Bambusa, Gigantochloa, and Dendrocalamus.

I found single almost ripe fruits on a plant of *Bambusa Tulda*, and on a *Gigantochloa*, which were flowering in the Botanic Gardens, Singapore, in 1945. These agreed together in essentials of structure, but did not agree with Gamble's statement for the Eubambuseae: "Pericarp thin, adnate to the seed." In both cases the apical part of the pericarp was thick and distinctly separate from the seed; the pericarp was much thinner toward the base of the fruit, but still easily separable from the seed, and the position of the embryo was not observable on the outside of the fruit. The

top of the fruit was abruptly narrowed to the style, the base only of which had become somewhat thickened. This structure agrees with that described by Gamble for *Dendrocalamus*, and with a fruit of *D. pendulus* Ridl. which I examined, except that the latter (as in some other species of *Dendrocalamus* described by Gamble) had the pericarp so thin near the base of the fruit that the position of the embryo could be seen. I therefore conclude that *Dendrocalamus* is not separable from *Bambusa* and *Gigantochloa* on fruit-characters.

The stamen-tube as a generic character.

Munro (10) and later authors have used the presence of a tube in place of free stamen-filaments as a character to distinguish genera, and Camus (3) even unites genera with stamen-tubes as a special subtribe. According to Gamble's generic diagnoses, a stamen-tube is present in *Gigantochloa* and *Oxytenanthera* and not in *Bambusa* and *Dendrocalamus*. But some species referred to *Oxytenanthera* have exactly the same spikelet-structure as those species of *Dendrocalamus* which have few florets; and two species included by Gamble in *Gigantochloa* (*G. heterostachya* and *G. latispiculata*) have in other respects the spikelet-structure of *Bambusa*. Further, united filaments occur in *Neohouzeaua* (Camus 3, Gamble 5), which in all other respects agrees with *Schizostachyum*, a genus which nobody considers related to *Gigantochloa*. It thus appears that united filaments have developed on at least three distinct evolutionary lines in the bamboos; therefore the character cannot be regarded as of basic importance in classification, and I doubt if it can be used to distinguish genera. I regard the subtribe Synandrae of Camus as a quite unnatural one.

Spikelet-structure in Bambusa, Gigantochloa, and Dendrocalamus.

It appears to me that the most significant feature of spikelet-structure in these genera is the development of the rachilla. In *Bambusa* the rachilla is elongate and jointed, with several internodes usually 2 mm. or more long, the lemmas of the fertile florets being all of about the same length. In the other genera the rachilla is very short, not jointed, the florets crowded closely upon it, the lower lemmas therefore shorter than the upper when several florets are present. On this basis it is easy to distinguish *Bambusa* on the one hand from *Gigantochloa*, *Oxytenanthera*, and *Dendrocalamus* on the other. A distinction on this basis involves the transfer of *Gigantochloa heterostachya* Munro and *G. latispiculata* Gamble to *Bambusa*, with which (as indeed Gamble realized) they agree in spikelet-structure, and I therefore propose the new binomials **Bambusa heterostachya** (Munro) comb. nov. (*Gigantochloa heterostachya* Munro in Trans. Linn. Soc. 26: 125. 1868) and **Bambusa latispiculata** (Gamble) comb. nov. (*Gigantochloa latispiculata* Gamble in Ann. Bot. Gard. Calcutta 7: 67. 1896).

We have now to distinguish between *Gigantochloa*, *Oxytenanthera*, and *Dendrocalamus*. Disregarding the stamen-tube (which is in fact sometimes

not at all easy to observe) and the fruit, we find that Gamble gives us very few other characters to use. Munro (10, p. 126) originally distinguished *Oxytenanthera* as having 1–3 florets, the palea (upper palea of Munro) of the uppermost or sole floret convex on the back, not keeled, the paleae of the lower florets (if present) 2-keeled; *Gigantochloa* had more florets, and the paleae all alike and 2-keeled. But Munro (and after him Gamble) included in *Oxytenanthera* the species *O. nigrociliata,* which had an imperfect uppermost floret described as unipaleate. The single organ present is called a palea by Gamble, but by its position I think it must truly be a lemma (lower palea of Munro); in any case it is quite unlike the true palea of the upper fertile floret in other species ascribed to *Oxytenanthera*, and is to me indistinguishable from the imperfect uppermost floret of species ascribed by Gamble to *Gigantochloa*. The two genera are in fact neither clearly distinguished nor clearly described by Gamble. As in *Oxytenanthera*, the palea of the uppermost perfect floret in *Dendrocalamus* is keelless, the paleae of the lower florets 2-keeled; Gamble states for some species that there may also be a small imperfect floret above the perfect ones.

I dissected spikelets of several species of *Gigantochloa* and *Dendrocalamus*, and of the Malayan species ascribed to *Oxytenanthera*, and found that Munro's distinguishing character, with slight emendation, is sufficient to separate *Gigantochloa* (including *Oxytenanthera nigrociliata* Munro) from the other two genera. In *Gigantochloa* there are always several fertile florets, all with 2-keeled paleae, and the spikelet is terminated by an imperfect floret consisting of a narrow lemma which is longer than all the other florets and usually projects slightly from the apex of a mature spikelet. In *Gigantochloa* also there is always (in my experience) a well-developed stamen-tube.

The distinction of *Oxytenanthera* from *Dendrocalamus* is not so easy. In both genera the uppermost fertile floret has an unkeeled palea, the lower florets (when present) have all 2-keeled paleae. In *Oxytenanthera* there are only 1–3 florets and there is no rudimentary terminal floret; in most species of *Dendrocalamus* there are more than 3 florets and there is sometimes a small rudimentary terminal floret. In *Oxytenanthera* there is a stamen-tube, in *Dendrocalamus* there is none. But what of *Dendrocalamus pendulus* Ridl. and a few allied species, which have one or two fertile florets, no rudimentary floret, and no stamen-tube? If we include these in *Dendrocalamus*, the distinction from *Oxytenanthera* on number of florets breaks down; if in *Oxytenanthera*, the distinction between the two genera rests only on number of florets, which is not satisfactory.

Vegetatively, all known species of *Oxytenanthera* (and *Dendrocalamus pendulus*) have relatively slender culms, often not strong enough to support their own weight, so that they rely on the support of neighbouring trees and may be described as semi-scandent. *Dendrocalamus*, on the other hand, has usually rather stout culms; but this does not apply to

D. strictus, and I doubt whether the character of slender as against stout culms could be used as a generic distinction. All things considered, I suggest merging *Oxytenanthera* with *Dendrocalamus*, pending further field study of the species.

The ovary of Schizostachyum.

Munro recognized that the ovary of *Schizostachyum* and other genera of his third group of bamboos was a peculiar structure. He wrote (10, p. 4): "The third division consists of berry-bearing Bamboos, in 8 genera. These are all extremely interesting from their peculiar fruit. The pistil generally appears to be contained in an envelope somewhat analogous to the sac, or utricle, or perigynium, which contains the seed of *Carex*. In the young state this is so closely attached to the style that it is almost impossible to separate it; in advancing to maturity it increases in various ways." Gamble was inconsistent in the terminology he used to describe this structure. Thus under *Teinostachyum Wightii* he wrote, "style included in the long beak of the perigynium," and under *T. Griffithii*, "ovary . . . narrowing into a long triquetrous beak forming the style."

I examined living flowers of *Schizostachyum brachycladum* (which flowers continuously in Singapore, but does not normally fruit), and dried flowers of other species, but saw no fruits. The ovary at flowering is slightly swollen, and is continued upward into a stiff angled style, with no sharp distinction between the two, and at the apex of the style are the short divergent stigmas. The style is hollow, with a free central strand of delicate tissue which is continuous below with the inner wall of the ovary, which surrounds the ovule. The annular hollow within the style is due to the breakdown of the thin-walled inner tissues, which do not keep pace in growth with the firm outer tissues. It is true that the stiff hollow style so formed is functionally somewhat similar to the utricle of *Carex*, though in homology and structure it is quite different. This peculiar style is the distinctive feature of all the later genera in Gamble's scheme. In *Dinochloa* the spikelets are very short, and the style also, but its structure appears to be the same; it has not however been well described, and I have seen no material.

Spikelet-structure of Schizostachyum.

In his work of 1896, Gamble does not appear to me to make a clear distinction between *Schizostachyum* and *Teinostachyum* (on p. 77 the spikelets of *Teinostachyum* are said to have one flower, on p. 97 many flowers); but in 1923 (5) he distinguishes the two by stating that *Teinostachyum* has several flowers in each spikelet, *Schizostachyum* only one. Now McClure has described a *Schizostachyum* with two florets in each spikelet (7); and I myself found that spikelets on plants of *S. brachycladum* growing in Singapore may have either one or two flowers. In such cases the palea of the lower floret is loosely convolute and usually distinctly 2-keeled toward the apex; that of the upper floret is tightly

convolute and hardly keeled. This not only does away with the distinction between *Schizostachyum* and *Teinostachyum*; it also breaks down their distinction from *Cephalostachyum*, which (according to Gamble's later paper) has a 2-keeled palea, whereas the others are said to have a palea convolute, not keeled. Indeed, Gamble himself was not consistent in this latter distinction, as in 1896 he described the palea of *Schizostachyum tenue* as 2-keeled. I suggest therefore that the genera *Schizostachyum*, *Cephalostachyum*, and *Teinostachyum* should be united; and probably *Pseudostachyum* should go with them.

The spikelets of *Schizostachyum* are articulate at the base of each floret, if there is more than one, as described by McClure (6, 8, 9), and the internodes of the rachilla are always long. Above the uppermost fertile floret the rachilla is extended to bear a more or less imperfect rudimentary terminal floret which is not jointed to it. In this character of articulation of the rachilla, *Schizostachyum* agrees with *Bambusa*, and I suggest that it is more likely to be related to *Bambusa* than to the *Dendrocalamus* group, with its very short unjointed rachilla.

Schizostachyum and Ochlandra.

The lodicules of *Schizostachyum* are relatively large, in the Malayan species usually 3 and sometimes more, often unequal in size, and there are sometimes intermediates between lodicules and stamens. I can see no sharp distinction on characters of lodicules and stamens between the one Malayan species included in *Ochlandra* by Gamble (*O. Ridleyi*) and those he places in *Schizostachyum*, and I would include *O. Ridleyi* in the latter genus; no fruits have been seen. The fruit of other species of *Ochlandra* may be distinctive, but it still lacks a proper description; and it is to be noted that McClure (8) has already united the small-fruited *Dinochloa* with the large-fruited *Melocalamus* (the two genera are placed in separate subtribes by Gamble), so size of fruit alone may not be a sufficient character on which to base generic separation. The only fruit of any of this group of genera which has been fully described is that of *Melocanna*, by Stapf (13).

Neohouzeaua, Dendrochloa, and Klemachloa.

These three genera, from Burma and Indo-China, appear to me redundant. *Neohouzeaua* Camus (2) admittedly differs from *Schizostachyum* only in the presence of a stamen-tube, and as above indicated I do not consider this a valid ground for generic distinction. I think that *Dendrochloa* Parker (11) also should be united to *Schizostachyum*; it has 5–7 florets in a spikelet, the paleae of the lower florets with 2 close keels, and the filaments of the stamens partially united (three together, two together, and one free). In spikelet-structure it shows no essential difference from the Malayan *Schizostachyum grande* Ridl. (of which I have examined type- and other material). *Klemachloa* Parkinson (12) is like *Dendrocalamus pendulus* Ridl. in spikelet-structure, having 1 or 2

florets, an unjointed rachilla, the uppermost or sole palea unkeeled, and free filaments; it has 2 or 3 lodicules, which are not found in *D. pendulus*, but are reported from a few species of *Dendrocalamus*. I would unite *Klemachloa* with *Oxytenanthera*, if that genus is maintained, or with a comprehensive *Dendrocalamus:*

Inter-relationships of bamboo genera.

Several authors have suggested that *Schizostachyum* and its allies, having (where present) large and sometimes numerous lodicules, in some cases quite large fruits and always a well-developed pericarp, and long rachilla-internodes, are the most primitive of existing bamboos. *Bambusa* agrees with these genera in its elongate rachilla-internodes, and in the almost universal presence of lodicules, but it differs in ovary-structure and in never having more than 3 lodicules, of which two are very fleshy like those of a great number of grasses. The short unjointed rachilla of *Dendrocalamus* and its allies seems likely to be derived from a primitive elongate state. In gross characters of ovary and fruit these genera do not differ appreciably from *Bambusa*, but more detailed study may indicate differences. I think it quite likely that *Bambusa* and *Dendrocalamus* represent distinct lines of advance from the primitive bamboo stock, from which *Schizostachyum* has changed less in inflorescence and floral structure.

A suggested re-classification.

Subtribe Melocanneae.

Ovary narrowed gradually into a stiff angled style which is hollow at flowering; fruit large or small, the pericarp free from the seed; spikelets 1- to many-flowered, the rachilla-internodes (if present) long, articulate; paleae of lower fertile florets (if present) more or less distinctly 2-keeled with keels close together; palea of uppermost (or sole) fertile floret tightly convolute; lodicules, if present, often large and flat, sometimes numerous.

Spikelets and style long (genera to be distinguished on fruit-characters?) *Schizostachyum, Ochlandra, Melocanna.*

Spikelets and style short .... *Dinochloa.*

Subtribe Bambuseae.

Ovary abruptly narrowed to a slender style which is not hollow at flowering; fruit small, with pericarp free from seed; spikelets usually many-flowered, with distinct articulate rachilla-internodes; uppermost floret (or florets) usually imperfect; lemmas all about equal; lodicules usually 3, of which 2 are very fleshy and different from the third; stamen-tube rare.

Florets many; palea not bifid.. *Bambusa.*

Fertile florets 3; lowest palea deeply bifid.................... *Thyrsostachys.*[1]

Subtribe Dendrocalameae.

Ovary and fruit as in Bambuseae; spikelets 1- to many-flowered, the rachilla very short, not articulate; lemmas in many-flowered spikelets very unequal, gradually longer toward apex of spikelets; uppermost floret perfect or imperfect, if perfect with an unkeeled palea, the other paleae 2-keeled; lodicules usually lacking, if present small; stamen-tube sometimes present.

All fertile florets with 2-keeled paleae; a terminal imperfect floret consisting of a long narrow lemma always present.............................. *Gigantochloa.*

[1] See N. L. Bor (1).

Uppermost or sole fertile floret with unkeeled palea, the paleae of remaining fertile florets 2-keeled; a terminal short imperfect floret present or not. *Dendrocalamus.*

(A possible distinction of *Oxytenanthera* from *Dendrocalamus* as follows:
Fertile florets 1–3, with no imperfect terminal floret; stamen-tube often present .... *Oxytenanthera.*
Fertile florets more than 3, with or without a short terminal rudimentary floret; stamens free.. *Dendrocalamus.*).

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DISTRIBUTION OF THE DIPTEROCARPACEAE

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There has been a good deal of study of this family during the past quarter century, and it is now possible to give a somewhat more detailed survey of its distribution than that made by Merrill in 1923 (6). Extensive studies of the family have been made in the regions where it is most highly developed. There have been changes in the notions of generic and specific limits, in records of distribution, and in the numbers of species recognized.

What was formerly recognized as the genus *Pachynocarpus* is now relegated to the status of a subgenus of *Vatica*. The genus *Balanocarpus* has been broken up and most of its species placed in *Hopea* or in *Shorea*. The only remaining species is *B. Heimii* King, which will need a new position. Two new genera, *Dioticarpus* and *Upuna*, have been described.

Brandis, in 1895 (2), listed some 325 species in this family, and about 220 of them are still regarded as good species. During the past half century, more than 200 additional species have been described, most of them from Western Malaysia. The principal publications in which the new species have been described are those of van Slooten (8–15), Symington (16–20), and Foxworthy (4, 5). These publications include the descriptions of more than 120 new species from Western Malaysia. Besides these there are scattered publications giving descriptions of new species from other parts of the range of the family, but these are relatively few in number.

I. GEOGRAPHIC DISTRIBUTION.

Six great regions of distribution are recognized, as follows: (1) Africa; (2) Ceylon; (3) India (Western Peninsula); (4) Eastern Peninsula or Further India; (5) Western Malaysia; and (6) Eastern Malaysia. Table I shows the distribution of the genera and species in the different regions. There are, as might be expected, transitional areas, where regions are adjacent or contiguous, and these will be noticed in discussing the different regions.

Region 1. Africa.

This great continent has been considered as outside the range of the typical representatives of the family. The genera *Marquesia*, with three species, and *Monotes*, with 31 species, are the only representatives known from Africa, and they are atypical and sometimes considered improperly placed in this family. However, the finding of fossil material of true

TABLE I.

GEOGRAPHIC DISTRIBUTION OF THE GENERA AND SPECIES OF DIPTEROCARPACEAE

Genus	Total spp.	Africa	Ceylon	India	Further India	Western Malaysia	Eastern Malaysia
Anisoptera	13				2	12	2
Balanocarpus	1					1	
Cotylelobium	5		1			4	
Dioticarpus	1			1			
Dipterocarpus	73		5	2	16	58	1
Doona	12		12				
Dryobalanops	9					9	
Hopea	73		4	8	13	49	4
Marquesia	3	3					
Monoporandra	2		2				
Monotes	31	31					
Parashorea	8				2	7	
Pentacme	3				1	3	
Shorea	131		5	3	20	107	3
Stemonoporus	14		14				
Upuna	1					1	
Vateria	5[1]		2	2			
Vatica	65		3	1	11	52	3
Totals	450	34	48	17	65	303	13

[1] Includes *Vateria Seychellarum,* which does not fit exactly into any of the regions and is not included in the other columns.

dipterocarp wood at Mount Elgon (Kenya-Uganda) and in Italian Somaliland has indicated that the subfamily Dipterocarpoideae was well represented in Africa in *late* Tertiary times. Bancroft (1) and Burtt Davy (3) have recorded the finding of additional material. The following quotation is from Bancroft.

> "It is, of course, well known to students of taxonomy and plant distribution that the typical living members of the *Dipterocarpaceae* are confined to Asia, their centre of distribution being most probably the 'Malaysian' area, from which distribution has taken place in a general north-westerly direction; and also that the family is represented in Africa only by an aberrant group, the *Monotoideae*, comprising some thirty species of *Monotes* and three of *Marquesia.* The members of this small group are not rain-forest trees, like the true Dipterocarps, but are scattered inhabitants of the savannah country at high altitudes and of acidic soil type . . . . it is evident that typical Dipterocarps were formerly more widely distributed than at the present day; and the inference is that, having reached Africa from Asia, they subsequently receded, leaving as representative of the family in Africa only the *Monotoideae*, which are well adapted to special conditions of habitat . . . . the former occurrence of true Dipterocarps in Somali-

land, and further to the southwest in British East Africa, when considered in relation to the present distribution of those living forms which they seem most closely to resemble, suggests that the extension of the family from Asia into Africa took place *by way of a north-western land-connexion between the two continents.*

"Other African fossil woods are now under consideration, and these, again taken into consideration with the present distribution of related forms, point to a similar conclusion of north-westward migration of Asiatic types. If such migration did in fact take place in Tertiary (or perhaps earlier) times, the climate of the then-existing land-connexion must have been much more humid than that of the corresponding area at the present day.

"Within the past few months, herbarium material has come to hand, from areas as far removed as Nigeria, Gabon, and the Belgian Congo, which indicates that *true* Dipterocarps (the sub-family *Dipterocarpoideae*) are still living in the primitive forests of Africa."

So far as known, the identifications of these recent collections have not yet been published.

The only possible transitional form that has been recorded between this region and the next is *Vateria Seychellarum* Dyer, from the Seychelles. This species seems to be closely related to its congeners in Ceylon and India.

The very distinct character of the hitherto recorded forms from Africa would seem to indicate that the African forms have long been separated from those of the regions to the east.

Region 2. Ceylon.

This island seems to constitute a very compact province of distribution. There are 48 species recorded, in nine genera, and only a single species, *Vatica chinensis* L., is known to have a range extending to India. Three genera, *Doona*, *Monoporandra*, and *Stemonoporus*, are known only from Ceylon. There is a higher proportion of endemism than is found in any of the eastern range of the family.

A few of the species of the larger genera (*Dipterocarpus*, *Hopea*, *Shorea*, and *Vatica*) show close relationship to other species of the same genera in India and Malaya.

All but one of the Ceylon species are found in the moister parts of the island. A single species, *Vatica obscura* Trimen, is recorded as characteristic of the drier part of the island.

Region 3. India (Western Peninsula).

This region, as indicated by Brandis, is bounded on the east by Assam, which is transitional to the next region.

The Indian region, as thus limited, contains but 17 species, 15 of them endemic. The small number of species may be due to the large areas of dry country and to unfavorable soil conditions. There are fairly extensive areas of tropical rain-forest, and all the species but *Shorea robusta* and *S. Tumbuggaia* are restricted to the moist regions.

The monotypic genus *Dioticarpus* is peculiar to a limited area in South India. *Vatica chinensis* L. is found also in Ceylon and *Shorea robusta* Gaertn. f. extends into Assam. *Dipterocarpus indicus* Bedd. is very closely related to *D. turbinatus* Gaertn. f., of the next region, and has sometimes been considered to belong to that species. *Shorea talura* Roxb. is very close to *S. floribunda* Kurz, of Burma, and possibly not distinct.

The transitional area of Assam is separated from India proper by mountainous country. Six species are represented in Assam, two of them endemic; one is Indian, and the others are found in the next region.

Region 4. Eastern Peninsula (Further India).

This includes Burma, Siam down to 10° N. lat., Indo-China, and the tropical portion of China. There is a great deal of mountainous country and the distribution of dipterocarps is limited by elevation and climate.

To the south there is land connection with the Malay Peninsula, which begins at the Isthmus of Kra, at about 10° N. lat. The Malay Peninsula is a part of Western Malaysia. There is a climatic change at about 7° N. lat., and few species cross this line. The area between 7° and 10° N. lat. is transitional between regions 4 and 5. South of 7° the flora is distinctly Malayan and north of 10° it definitely belongs to region 4. In recent geologic time, the Malay Peninsula south of 7° was an island.

Within region 4 are found most of the species that show distinct adaptation to a prolonged and severe dry season. There are also considerable areas of rain-forest, where the conditions approach those of the next region and are most favorable for the development of dipterocarps. Of the 65 species recorded from region 4, 31 are endemic. Most of the species are in the moister parts.

The most striking feature of the distribution of dipterocarps in this region is what has been called the *dry deciduous dipterocarp forests* of Burma, Siam, and Indo-China. These forests are extensive and are most often found on laterite, though sometimes on sandy or gravelly soil. The dominant and strikingly gregarious species are *Dipterocarpus tuberculatus* Roxb., *D. obtusifolius* T. & B., and *Pentacme suavis* A. DC. The last named species occurs in the driest situations and often on other soils than laterite. It has been found on calcareous soil and as far south as 7° N. lat.

The species of the dry deciduous forests usually have a thick bark, which enables them to resist ground fires.

Region 5. Western Malaysia.

This includes the Malay Peninsula, the part of the Malay Archipelago west of Wallace's Line, and the Philippine Islands. The land is generally covered with tropical rain-forest, soil and climate being most favorable to the development of high forest. The most representative species of these forests are members of the family Dipterocarpaceae, which usually provide the largest volume of timber. Fully two-thirds of the species of

the family are found in this region. Twenty-four of the species extend into region 4 and only two species into Eastern Malaysia.

The genera *Dryobalanops*, *Balanocarpus*, and *Upuna* are known only from this region; and all of the larger genera of the family also have their greatest development in this region. What was formerly regarded as the genus *Isoptera* is now considered to be a section of the genus *Shorea*.

Table II shows the distribution of species and genera in the different parts of Western Malaysia.

TABLE II.

Genus	Malay Peninsula	Sumatra	Java	Borneo	Philippines	Total spp. W. Malaysia
Anisoptera	7	4		3	4	12
Balanocarpus	1					1
Cotylelobium	2	2		3		4
Dipterocarpus	24	22	5	34	11	58
Dryobalanops	2	2		9		9
Hopea	25	8	1	20	9	49
Parashorea	4	3		2	2	7
Pentacme	1				2	3
Shorea	54	22	1	60	15	107
Upuna				1		1
Vatica	21	10	3	21	8	52
Totals	141	73	10	153	51	303

This region is generally considered to be the centre of distribution of the family. The great island of Borneo has the largest number of species and the Malay Peninsula only slightly less. Considerable parts of Borneo are very imperfectly known botanically, and it is probable that the number of species from the island will be considerably increased. Of the 153 species found in Borneo, 52 are known from the Malay Peninsula, 33 from Sumatra, 15 from the Philippines, three from Java, and two from Eastern Malaysia.

It seems that Sumatra, the Malay Peninsula, and the Philippine Islands have had former land connections with Borneo and that this land was the region where the family originated and from which it spread out.

The most widely distributed species are: *Dipterocarpus grandiflorus* Blanco, from Burma, Siam, the Malay Peninsula, Sumatra, Borneo, and the Philippines; *D. gracilis* Bl., from Assam, the Malay Peninsula, Sumatra, Java, Borneo, and the Philippines; and *Shorea guiso* (Blanco) Bl., from Indo-China, Siam, the Malay Peninsula, Borneo, and the Philippines.

Region 6. Eastern Malaysia.

This includes that part of the Malay Archipelago east of Wallace's

Line, — extending as far to the east and south as the great island of New Guinea. It is an extensive area, but contains very few representatives of this family, — a total of 13 species, as follows:–

Anisoptera — two species. One of these, *A. costata* Korth., is widely distributed in Western Malaysia. The other is restricted to New Guinea.

Hopea — four species in New Guinea, one of them also in Celebes.

Shorea — three species — one in New Guinea, one in the Moluccas, and one in Celebes and the Moluccas.

Vatica — three species — one of wide distribution and two restricted to Celebes. The species of wide distribution, *V. papuana* Dyer, seems to be adapted to distribution by sea-currents. It is found along the coasts of the southern Philippines, East Borneo, the Moluccas (Ternate, Obi, Batjan, Aru Islands), and New Guinea.

Dipterocarpus — a single species, *D. retusus* Bl., as far to the east as Sumbawa.

It would seem that the barrier indicated by Wallace's Line (or its modification by Merrill) has been sufficient to prevent the spread of many species to this region.

Van Slooten (14, p. 434), impressed by the finding of two species of *Dipterocarpus* in Bali and one species in Sumbawa, stated, " . . . it is certain that the distribution of the genus *Dipterocarpus* has nothing to do neither with a line of demarcation through Central Java, nor with the so-called line of Wallace."

Nevertheless, it seems to me that this line is important and marks the limit beyond which few species of dipterocarps have gone.

II. LATITUDINAL RANGE.

The family is, as is well known, a tropical one and has its best development in the equatorial region. A few species extend to the northern limits of the tropics and have an extreme range to a short distance outside the tropics. The known species with such distribution are:–

In India — *Shorea robusta* Gaertn. f. — to 32° N. lat.
In Burma — *Dipterocarpus tuberculatus* Roxb. — to 25° N. lat.
D. obtusifolius T. & B. — to 24° N. lat.
Shorea obtusa Wall. — to 24° N. lat.
Pentacme suavis A. DC. — to 25° N. lat.

III. ALTITUDINAL RANGE AND SOIL CONDITIONS.

Most species are found in lowland forest, usually below 2,000 ft. The highest elevation recorded is a little over 5,000 ft. This has been recorded for *Shorea robusta* and for two species of *Dipterocarpus*.

Certain species are usually found on low ridges, and certain others are usually found at the higher elevations. However, characteristically high hill forms are sometimes found at lower elevations, and the lowland forms may be found up to 2,500 feet or more, apparently depending upon conditions of exposure and drainage.

Soil conditions influencing distribution.

The relatively small numbers of species found in dry or deciduous forests

are greatly influenced by the nature or condition of the soil. The most characteristic case is that of *Dipterocarpus tuberculatus* Roxb., which is most often found on lateritic soil. Other species characteristic of the dry deciduous forests have been mentioned. *Shorea robusta* Gaertn. f. thrives on moist deep sandy loam with good subsoil drainage. It may occur on several types of soil, but it needs moist soil and good drainage.

Most species of dipterocarps occur in tropical rain-forest, where there is a good deal of soil moisture and high humidity. Under these conditions, the nature of the soil is of less importance. Drainage is, however, important. Most species, while requiring a good deal of moisture, do not thrive in a water-logged or swampy soil. Nevertheless, there are a number of species which thrive in fresh water swamps. Some of the species found in fresh water swamps, or at the edge of the swamp, and their distribution, are:–

Anisoptera marginata Korth. — Malay Peninsula, Sumatra, Bangka, Borneo.
Dipterocarpus costulatus v. Sl. — Malay Peninsula, Sumatra, Borneo.
Dipterocarpus Dyeri Pierre — Burma, Indo-China, Malay Peninsula.
Dryobalanops Rappa Becc. — Borneo.
Shorea albida Sym. — Borneo.
S. Pinanga Scheff. — Borneo.
S. Teysmanniana Dyer — Malay Peninsula, Sumatra, Borneo.
S. platycarpa Heim — Malay Peninsula, Borneo.
S. rugosa Heim — Borneo.
S. uliginosa Foxw. — Malay Peninsula, Sumatra.
S. inaequilateralis Sym. — Borneo.
Vatica imbricata v. Sl. — Borneo.
V. Wallichii Dyer — Malay Peninsula, Sumatra.

IV. METHODS OF DISTRIBUTION.

1. *By water.*

A few species seem to be adapted to distribution by water. The single species believed to be distributed by sea-currents, *Vatica papuana* Dyer, has already been mentioned.

Several species of river valleys are believed to be distributed by fresh water. Examples are *Shorea seminis* (De Vr.) v. Sl. and *S. sumatrana* (Thor.) Sym.

2. *By wind.*

Most species have fruits that are equipped with wings several times longer than the seed. These wings aid in the dispersal of the fruits by wind action.

The rain-forest, where most of the species grow, is so dense that there is comparatively little action by strong winds within the forest and there is consequently little opportunity for distribution to long distances. Ridley (7, pp. 104-109) has stated that dipterocarp fruits are usually not carried by wind to a distance of more than 30 or 40 yards from the parent tree, and, exceptionally, to only about 100 yards.

This statement may be rather too conservative, in that it does not give sufficient importance to the occasional wind storm. Webber (21) has given an account of a small wind storm, in the Malay Peninsula, that carried large numbers of dipterocarp fruits to a height of several hundred feet and a distance of at least half a mile. Forms represented among the fruits thus carried were: — *Shorea leprosula*, *S. parvifolia*, *S. macroptera*, *S. bracteolata*, *Anisoptera* spp., *Dipterocarpus* spp., and *Hopea* spp.

Similar observations have been made in the Philippine Islands, where fruits of *Parashorea plicata* Brandis were carried to distances in excess of a half-mile by typhoon winds.

Such wind storms as those mentioned are, doubtless, infrequent, but may occur a number of times during the life of a tree. It is evident that wind is an important agency in the distribution of members of this family.

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PARALLEL AND CONVERGENT EVOLUTION IN FERNS

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WHATEVER the details of its technique, evolution is accepted by the world as the general process by which the countless kinds of living things have been derived from comparatively uniform remote ancestors, and finally perhaps from one single living thing. This has been in general a process of differentiation. It has been so also in detail, as each kind of living thing originated from a more or less different parental kind or species. We are so used to regarding evolution as a process of differentiation that if a botanist or zoologist be asked as to the occurrence of convergent evolution, by which similar or apparently identical creatures are evolved from different ancestors, he is likely to reply that it is theoretically possible, but that he knows of no recognized instance. He may add that if such a procedure did occur in nature, we might not recognize it, but that it would be interesting if we could demonstrate it.

However, as a general proposition, some measure of convergent evolution is not only not rare, but is familiar, if one will but consider what one knows. Dry lands the world over receive immigrants from more humid lands, which undergo similar modification in adaptation to the dry climate. Dry-land plants of the most diverse ancestry thus evolve small, harsh leaves. Many Euphorbiaceae have evolved the form and much of the structure more familiar in the cacti. Dwarf species inevitably lose some of the structures of their larger ancestors, with loss of size. The most universally familiar example of this phenomenon is the loss of structure by parasites, and the resulting resemblance of plants quite regardless of the differences between their ancestors. Plants of many families have undergone in common the loss of leaves and of chlorophyll in becoming parasites. This evolution is convergent or parallel; there is no essential difference. The possibility that present resemblance may blind us to diverse ancestry is shown by the fact that we hold our predecessors of a few years to have been deceived in this way. We recognize more families of parasites than were known some years ago, because we believe that the old families contained unrelated, even if similar, elements.

The ferns are better known, as to their geography and their real affinities, than is any other group of similar size. None is a parasite, and few are dry-country plants. In the light of our present understanding of the relationships of the genera, we now recognize among them numerous instances of parallel and convergent evolution. As recently as the period when the elders among us began to study ferns, their classification by Sir William Hooker was accepted with little question throughout the world.

As Sir William was one of Darwin's influential supporters, this should not have been the expression of a purely pre-Darwinian viewpoint. The Synopsis Filicum of Hooker and Baker recognized 58 genera of Polypodiaceae. One of the greater of these was *Acrostichum*, including almost all ferns with the sporangia spread over the backs of the fronds, — not in discrete clusters, called sori.

Of the 172 species of *Acrostichum* in the 1874 edition of Synopsis Filicum, only (1) *A. aureum* retains to-day that generic name; it is probably a relative of *Pteris*. *Acrostichum pteroides*, now *Neurosoria pteroides* (2), is a little known Australian species related to *Cheilanthes*, perhaps belonging in that genus. *Acrostichum requiniana* is now (3) *Taenitis requiniana*, an imperfectly acrostichoid derivative of the widespread *T. blechnoides*.

Acrostichum apiifolium, endemic in the Philippines, is a descendant of *Dryopteris*,[1] now called (4) *Psomiocarpa apiifolia*, a name given in 1849 but rejected by Hooker and Baker. The Cuban *A. aspidioides* is a very similar independently derived dryopterid fern, now called (5) *Atalopteris aspidioides*. For *A. auritum*, the name (6) *Stenosemia aurita*, given in 1836, has been restored; it is descended from *Dryopteris* through an intermediate genus, *Heterogonium*. Also derived from *Dryopteris*, but from a different part of the genus, is (7) *Quercifilix zeilanica*, called *Acrostichum quercifolium* by Hooker and Baker. Baker later described as *Acrostichum* three species (*A. celebicum*, *A. exsculptum*, and *A. oligodictyum*) now recognized as (8) species of *Dryopteris* (or better, of *Cyclosorus*), all imperfectly acrostichoid in fruit. *Acrostichum Harlandii* and *A. taccaefolium* are species of (9) *Hemigramma*, derived from *Tectaria*, of more remote dryopterid origin.

Acrostichum scandens is now (10) *Stenochlaena palustris*, not clearly related to any other fern here mentioned. *Acrostichum sorbifolium* has been called *Stenochlaena* by some more recent authors, but is better distinguished as (11) *Lomariopsis*. Confused with *A. scandens* in the Synopsis was a very different fern, (12) *Teratophyllum aculeatum*; except that the resemblance is not sufficient to justify Hooker's confusion, we would have here a fine illustration of generically distinct ferns masquerading as specifically identical. *Acrostichum Blumeanum* is now a (13) *Lomagramma*. *Acrostichum articulatum* and *A. Wilkesianum* have also been called *Lomagramma*, but are better distinguished as (14) *Arthrobotrya*. The evolution of these four or five genera has been so convergent that there is to-day no agreement as to their real affinities; but it is agreed that *Stenochlaena*, *Lomariopsis*, *Teratophyllum*, and *Lomagramma* are distinct from one another as well as from *Acrostichum*.

A considerable number of former *Acrostichum* species are now regarded

[1] To avoid a less familiar name, I use *Dryopteris* here in the sense of Christensen's Index Filicum.

as (15) *Bolbitis*, a pantropic genus. An oriental relative of *Bolbitis* is (16) *Egenolfia*, represented in the Synopsis as *A. appendiculata*. Roughly half of the *Acrostichum* species of the Synopsis are now (17) *Elaphoglossum*, a very large genus in all warm countries. Derived from *Elaphoglossum* are (18) *Microstaphyla* and (19) *Rhipidopteris*, each represented by one species of *Acrostichum* in the Synopsis. These five genera have in common a striking spore character, indicating that they are related, mutually and to other ferns recently mistakenly placed in *Dryopteris*.

Acrostichum bicuspe is (20) *Cheiropleuria bicuspis*, a Malayan fern so peculiar that it has been proposed to make it a family by itself. Related to it, however, is (21) *Christiopteris tricuspis*, *A. tricuspe* of the Synopsis. *Acrostichum spicatum* and *A. platyrhynchos*, now called (22) *Belvisia* (or *Hymenolepis*), may be a third surviving branch of the same old group.

Of the polypodioid ferns, *Acrostichum axillare* is (23) *Leptochilus axillaris*, which is so deceptively like *A. lanceolatum*, a (24) *Dendroglossa*, that botanists as keen as Christensen and Ching have been unable to see that they are generically distinct. Under *A. variabile*, Hooker and Baker combined one or more species of *Dendroglossa* with (25) *Leptochilus*[2] *decurrens*, which I am sure is of independent immediate ancestry. *Acrostichum rigidum* is (26) *Photinopteris speciosa*, derived through *Aglaomorpha* from *Microsorium*, which is the immediate parent of *Leptochilus*. *Acrostichum drynarioides* is now (27) *Merinthosorus*, likewise derived from *Aglaomorpha*.

In running through this list, I have overlooked three American genera, (28) *Trachypteris*, (29) *Neurocallis*, and (30) *Polybotrya*.

Platycerium is also perfectly acrostichoid in its fructification, but for other reasons Hooker and Baker held it generically distinct.

It will help to show the diversity of origin of the foregoing list of genera if they be now tabulated in their most recent systematic arrangement.

PTERIDACEAE	
Taenitis requiniana	*Acrostichum requinianum*
Neurocallis praestantissima	*A. praestantissimum*
Acrostichum aureum	*A. aureum*
Neurosoria pteroides	*A. pteroides*
Trachypteris aureo-nitens	*A. aureo-nitens*
ASPIDIACEAE	
Polybotrya osmundacea	*Acrostichum osmundaceum*
Bolbitis serratifolia	*A. serratifolium*
Egenolfia appendiculata	*A. appendiculatum*
Lomariopsis spp.	*A. sorbifolium*
Teratophyllum spp.	*A. sorbifolium*
Arthrobotrya articulata	*A. articulatum*
Lomagramma spp.	*A. Blumeanum*

2 *Leptochilus decurrens* is the name in present use for this species, but it is improper because the species is of different immediate ancestry from *L. axillaris*, the type of *Leptochilus*. A new generic name is provided for it in my Genera Filicum, now in press.

Elaphoglossum spp.	*Acrostichum* spp.
Microstaphyla furcata	*A. bifurcatum*
Rhipidopteris peltata	*A. peltatum*
Psomiocarpa apiifolia	*A. apiifolium*
Atalopteris aspidioides	*A. aspidioides*
Stenosemia aurita	*A. auritum*
Hemigramma taccaefolia	*A. taccaefolium*
Quercifilix zeilanica	*A. quercifolium*
BLECHNACEAE	
Stenochlaena palustris	*Acrostichum palustre*
POLYPODIACEAE	
Cheiropleuria bicuspis	*Acrostichum bicuspe*
Christiopteris tricuspis	*A. tricuspe*
Belvisia (Hymenolepis) spicata	*A. spicatum*
Platycerium spp.	*Platycerium* spp.
Leptochilus axillaris	*Acrostichum axillare*
Leptochilus decurrens	*A. variabile*, in part
Dendroglossa minor	*A. minus*
Merinthosorus drynarioides	*A. drynarioides*
Photinopteris speciosa	*A. rigidum*

I may not apologize for the length of this list of names, uninteresting to the pteridologically illiterate, even if musical, because the length of the list is the point I emphasize, and have repeated for the sake of emphasis. The list might be made much longer, if, instead of confining myself to Hooker, I went back to Swartz, and to Linnaeus, whose definition of *Acrostichum* was substantially the same as Hooker's. Including their species, the number would have been more nearly fifty of to-day's genera, almost all representing the same kind of convergent evolution.

The acrostichoid fructification is usually associated with the evolution of dimorphic fronds, — different vegetative and fertile fronds, — the fertile ones usually restricted in area, longer-stalked, and shorter-lived. Some degree of dimorphism of fronds, or of parts of fronds, has been evolved independently along a considerably greater number of lines; but dimorphism did not happen to be a primary element in generic definition, and so the ends of the resulting phyletic series escaped combination on this ground.

The Synopsis Filicum maintains a genus *Gymnogramma* of about 100 species, including most ferns with the sporangia in extended lines along the veins and without protective covering, but not on the area between the veins, where their presence would have thrown the plants into *Acrostichum*. These hundred species are now distributed among the following 23 genera:– "*Dryopteris*," *Heterogonium*, *Woodsia*, *Athyrium*, *Ceterach*, *Aspleniopsis*, *Syngramma*, *Craspedodictyum*, *Pterozonium*, *Coniogramme*, *Hecistopteris*, *Gymnopteris*, *Gymnogramma*, *Pleurosorus*, *Eriosorus*, *Bommeria*, *Anogramma*, *Trismeria*, *Pityrogramma*, *Loxogramme*, *Colysis*, *Selliguea*, and *Pleopeltis*. Because some of these genera include more than one independent instance of such evolution, because the Synopsis treats as genera (*Meniscium*, *Hemionitis*) some such series, and because of several

such cases unknown to its authors, the actual number of independent evolutionary series converging to the *Gymnogramma* type of fructification is again far more than thirty.

The feature in which parallel evolution has occurred in the largest number of cases is the loss of the indusium. Failure to recognize this by taking account of ancestry was responsible for the monstrous "genus" *Polypodium*; within restricted ranges, for such temporarily respected genera as *Phegopteris*, *Goniopteris*, and *Alsophila*. Presentation of individual cases would involve discussion of species rather than genera, and would require far more space than is available here.

Limiting myself to genera, I will close with two especially interesting cases.

The pair of genera *Cochlidium* and *Scleroglossum* present an exceptional case of convergent evolution. The former has ten named species in tropical America; the latter, seven, from Ceylon to Polynesia. They are tiny ferns with densely clustered thick, linear fronds, with one linear sorus on each side of the midrib in the upper part of the frond. They are so alike that care is required to distinguish the species in the two hemispheres. Their geographical isolation made their generic identity doubtful, but a detailed anatomical study by Goebel made him conclude that there was no sufficient ground for their separation. Before and after his study, I was forced to the same conclusion; the more reluctantly the second time, because Goebel had also established the common descent of the American *Cochlidium* and *Xiphopteris*, and Maxon had previously shown that *Xiphopteris* was too intimately connected with its local neighbors, pinnate ferns called *Polypodium*, or preferably *Ctenopteris*, to require recognition as a genus. This established *Cochlidium* as a genus of American origin, and no other genus of demonstrable American origin was known in the Malay region.

And then, a New Guinea plant named "*Polypodium pleurogrammoides*" came to hand. Let its generic name be what it will (it can be *Nematopteris*, or *Grammitis*), it shares the characteristics of *Scleroglossum* and *Grammitis*, and illustrates the derivation of the former from the latter. The proof is provided by microscopic features of identity, but is sufficient. *Cochlidium* is descended from pinnate ferns; *Scleroglossum* from a genus with simple fronds. But convergent evolution produced genera so identical that neither Goebel nor I could find a satisfactory distinction, though antecedent probability made us expect one. Christensen has later found a second microscopic difference.

Phyllitis Scolopendrium, longer known as *Scolopendrium vulgare*, the "hart's tongue fern," occurs well around the North Temperate zone. Its sorus is "double"; that is, each of two neighboring veins produces a long sorus, on the side facing the other vein, and the indusia are broad enough either to meet, or to come near enough to doing so that the result looks like one sorus. The genus is derived from *Asplenium*. The North Amer-

ican *Asplenium pinnatifidum*, which suggests *Scolopendrium* so strongly that Diels transferred it to that genus, may represent its parentage in *Asplenium*. *Phyllitis* is clearly of northern origin, and is probably not at all ancient.

Scolopendrium Durvillei Bory was described from the New Guinea region. Though misunderstood by Baker and made the basis of another genus, *Diplora*, it has exactly the soral character of *Scolopendrium*. Its approximate ancestor in *Asplenium* is *A. epiphyticum*, not more nearly related to *A. pinnatifidum* than it must be as an *Asplenium*. If not *Asplenium*, *Scolopendrium* and *Diplora* must be two genera, distinguishable by description solely by the base of the lamina, cordate in one, cuneate in the other. This would be unsatisfactory if it were the whole story.

But we know now not merely two, but six instances in which convergent or parallel evolution has produced from *Asplenium* the sorus of *Scolopendrium*:

Asplenium Scolopendrium L.
Scolopendrium Durvillei Bory, the preferable name of which seems to be *Asplenium scolopendropsis* F. v. M.
Scolopendrium Delavayi Franch., preferably *Asplenium Delavayi*.
Scolopendrium cardiophyllum Hance, made a distinct genus, *Boniniella* by Hayata, but better treated as *Asplenium*.
Antigramma Presl, of Brazil, usually called *Scolopendrium*.
Schaffneria nigripes Fée, of Mexico, known also as *Scolopendrium* and *Phyllitis*.

If a summary be desired:

Parallel and convergent evolution are really common phenomena in ferns.

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"NOTHOLAENA" IN BRAZIL

C. A. Weatherby

With two plates

Most American species of the complex traditionally referred to *Notholaena* are Cordilleran. Their aggregate range extends, in a relatively narrow belt limited by the extent of the highlands which offer the dry and rocky habitats congenial to these xerophytes, from the southwestern United States to northern Argentina and Chile. One species, *N. dealbata* (Pursh) Kze., occurs in the western half of the Mississippi Basin in the United States; three are endemic in the West Indies; two, *N. obducta* (Mett.) Baker and *N. Hassleri* Weath., extend to low elevations in the basin of the Paraná; and in the highlands of eastern Brazil, mostly in the states of Minas Geraes, Goyaz, and Piauhy, is found a group of five endemic species (plus a few isolated stations for two varieties of *N. nivea*). Of these outliers, the populations of the Mississippi Basin and of the West Indies are clearly members of otherwise Andean groups. In South America, *N. Hassleri* and *N. obducta* show less close, but still recognizable relationship, the former with *N. sinuata* (Lag.) Kaulf. of wide Andean range, the latter with *N. squamosa* (Gill.) Lowe of Bolivia and northern Argentina. But the five endemics of eastern Brazil are both geographically and morphologically isolated.

Judging from their scanty representation in herbaria, all the east-Brazilian species are rare and local. Although St. Hilaire collected members of the group about 1817, only two species, *N. Pohliana* Kze. (1840) and *N. eriophora* Fée (1850-52), were recognized until 1896, when Taubert added *N. goyazensis*; and nothing resembling a study of the group was made until 1940, when Brade proposed *N. venusta* and gave a key to the whole five.

Brade's knowledge of Brazilian ferns is unsurpassed; that I venture to follow his sketch with discussion of my own is because he goes very little into detail; because I can, I hope, add data inaccessible to him; and because certain points of classification, identity, and nomenclature remain to be considered. They are not all settled here; but it seems worthwhile to set down the information I have, as a step toward better understanding of these still little-known ferns.

Four of the east-Brazilian endemics (*N. venusta*, *N. eriophora*, *N. goyazensis* and *N. geraniifolia*) are closely related and in many ways alike. All have short-repent, often branched rhizomes. The rhizome-scales are narrow, with a weak capillary tip often tortuous in dried material, a more

or less developed castaneous, sclerotic central band, and a narrow, brownish, hyaline margin. The fronds are approximate, forming loose tufts. The blades are more or less strongly pedate; under conditions of drought they curl up into tight little balls with only the lower surface, well protected against excessive transpiration by its tomentum, exposed. Unfortunately for the herbarium-worker, most specimens have been collected in this condition. The indument is lanate and, at least on the lower surface, very dense. In three species it is composed of a close felting of very fine hairs next the leaf-surface, overlaid by longer and coarser hairs, quite like a muskrat's fur. The sori are borne on more or less dilated, clavate or somewhat flabellate vein-ends at or near the margin. The sporangia are of the usual cheilanthoid type — short-stalked, with a narrow ring and a broad stomium of laterally much elongated cells.[1] The spores are also of the type commonest in the Cheilantheae, subglobose and smooth or minutely granular.

The four species have their nearest and their only close relative in *N. inaequalis* Kze. of southern Africa (Cape Colony to Natal, Rhodesia, and Angola), as Kunze himself suggested in describing that species. This is, of course, one more example of a geographic relationship often noted in other groups. In indument and position and structure of sori *N. inaequalis* is quite like its Brazilian brethren, but in it the pedate habit is less developed and the rhizome-scales are larger and of different structure.

In the fifth east-Brazilian species, *N. Pohliana*, rhizome, scales, and sori are similar to those of the other four. But the architecture of the lamina and the indument are quite different, and the pinnules have a very narrow, but definite, hyaline marginal band, expanded into small lobes opposite the soriferous vein-ends — an obvious development in the direction of the false indusia of *Cheilanthes*. Band and lobes are ciliate. Like the others, *N. Pohliana* appears to have no close relatives among Andean species. *N. cinnamomea* Baker of Central America resembles it in habit and indument, but has the leaf-margin quite unmodified and the sori somewhat elongate and borne on scarcely dilated vein-ends a little back from the margin. Christensen (Ind. Fil. 462) has suggested that *N. Pohliana* might be better placed in *Adiantopsis*. Very possibly its affinities do lie with a group of species of Brazil, northern Argentina, and areas between. variously referred to *Adiantopsis* and *Cheilanthes*, such as *A. regularis* (Kze.) Moore and *C. Regnelliana* Mett. These species may eventually be brought together as one of the units in the final arrangement of the Cheilantheae.

The taxonomic treatment which follows is based on material in eleven herbaria, the European visited in 1937 and 1939. They are: Berlin (ab-

[1] They are well figured in Mart. Fl. Bras. 1(2): *pl. 66.*

breviated as B); British Museum (BM); Field Museum (F)[2]; Geneva (Gen); Gray Herbarium (G); Kew (K); New York (NY); Paris (P); Philadelphia Academy (Pa); United States National Herbarium (US); Yale University (Y). To the officers of all of them I am greatly indebted for the privilege of examining the specimens under their care — a privilege particularly valuable in a group so inadequately represented in most single herbaria as this.

Characters given in the introduction or in the key are, for the sake of brevity, usually omitted in the descriptions. Many of the place-names, quite unfamiliar to me, were perforce copied, as best I could, from handwritten labels in European herbaria. I have tried to check them with standard atlases (in which they are very often not to be found) and with the recent Millionth Maps of the American Geographical Society (where also I have sometimes failed to find them). If, under these circumstances, I have been guilty of any particularly grotesque mis-spellings or misplacing of localities. I can only beg the indulgence of my South American colleagues.

As in previous papers — Contrib. Gray Herb. 127: 3–15 (1939); Lilloa 6: 251–275 (1941) — the name *Notholăena* is retained in its traditional broad sense pending a thorough study of all the species concerned.

KEY TO THE BRAZILIAN SPECIES REFERRED TO NOTHOLAENA.

a. Indument of hairs. *b*.
 b. Lamina deltoid or pentagonal, pinnate-pedate or pedate, usually much shorter than the stipe; lowest pinnae much the largest, usually strongly inequilateral. *c*.
  c. Stipe thinly villous with straight, distinctly moniliform, often gland-tipped hairs; lamina with 1–3 wholly free pinnae, the rachis between them not winged; only the basal pinnae deeply divided.............1. *N. venusta*.
  c. Stipe lanate with long, tortuous, matted, slender, non-glandular hairs, or glabrous; all segments of the lamina usually connected at least by a narrow wing along the rachis. *d*.
   d. Indument of both surfaces of lamina of long, slender, tortuous, obscurely articulate hairs; only the basal segment deeply lobed.....2. *N. eriophora*.
   d. Indument of lower surface of lamina of fine, short, densely felted tomentum overlaid by long, straightish, conspicuously articulate hairs, the cross-walls of their cells dark; median segments, as well as the basal, lobed. *e*.
    e. Indument of upper surface of lamina of fine, whitish, tortuous, more or less matted hairs; median segments simply pinnatifid, with entire lobes; rhizome-scales bright brown in mass.................3. *N. goyazensis*.
    e. Indument of upper surface of lamina of coarse, straightish, golden to whitish, not much matted hairs; median segments sub-bipinnatifid, their lobes more or less cut; rhizome-scales fuscous in mass. 4. *N. geraniifolia*.
 b. Lamina deltoid-lanceolate, bipinnate, equalling or longer than stipe; lowest pinnae not greatly larger than those adjacent, equilateral; indument of lower surface of lamina thin.......................................5. *N. Pohliana*.
a. Indument ceraceous; lamina at least subtripinnate. *f*.

[2] Now the Chicago Natural History Museum, but known so long under its old title that it seems more convenient and intelligible to retain the abbreviation "F" for the present.

f. Indument white; stipe bright-castaneous; lamina bipinnate above, subtripinnate in lower pinnae..............................6a. *N. nivea* var. *oblongata*.
f. Indument yellow; stipe dark-castaneous; well-developed lamina fully tripinnate. 6b. *N. nivea* var. *flava*.

1. **Notholaena venusta** Brade in Anais Prim. Reun. Sul-Amer. Bot. 2: 7, *t. 4, fig. 1, 2* (1940). PLATE I, FIG. 1.
Notholaena capillus St. Hilaire in herb. and ex Christ in Bull. Herb. Boiss. II. 2: 381 (1902), pro syn.

Rhizome about 2 mm. in diameter, its scales about 2 mm. long, sometimes serrulate toward the apex with narrow, ascending teeth; stipe terete, 0.4–0.5 mm. in diameter, 6.5–9 cm. long, castaneous, shining; lamina pentagonal to somewhat elongate-deltoid, 3–4 cm. long, 2–3 cm. wide, commonly fully pinnate to about the third pair of pinnae from base; basal pair of pinnae deeply pinnatifid and more or less inequilateral by the elongation of the basal segment on the lower side, their divisions oblong, obtuse, entire or the developed basal segment shallowly undulate-lobed; median pinnae oblong or linear-oblong, entire or shallowly lobed, rather distant, decreasing rather gradually to a somewhat prolonged, obtuse, narrow, pinnatifid apex; rachis castaneous; tomentum of the upper surface of lamina grayish, of slender, tortuous and matted long hairs, that of the lower surface rufous, of similar hairs underlaid by a dense felt of shorter and finer hairs; veins immersed, ultimate veinlets 1–2-forked, at least the soriferous with rather abruptly dilated, somewhat flabellate ends at or very near the margin; spores about 65 μ in diameter. — Known to me from Minas Geraes and Piauhy.

TYPE: Ad rupes, Diamantina, Minas Geraes, June, 1934, *Brade 13494* in herb. Jardim Botanico, Rio de Janeiro; not seen.

Specimens seen. MINAS GERAES: Sub rupibus prope pagum Nossa Senhora da Penha, *St. Hilaire B' 1220* (P)[3]; Serra de Ibitipoca, June, 1896, *herb. Magalhães Gomes 1099* (P); Serra do Cipó, June, 1901, *Schwacke 14520* (G, P). PIAUHY: Without definite locality, 1836, *Gardner 2392* in pt. (P).

Both St. Hilaire, who made the first collection of this "especie graciosa," as Brade appropriately calls it, and Christ gave it herbarium names. Christ suppressed his own, but mentioned St. Hilaire's as a synonym of *N. eriophora*. I used *N. capillus* in labelling sheets at Paris; it must now give way to the properly published *N. venusta*.

Both *N. venusta* and *N. eriophora* have had the misfortune to be described from depauperate specimens, as will appear on comparison of the drawing from an average specimen of St. Hilaire's, reproduced here, with

[3] St. Hilaire in his Travels mentions two villages by this name, both in Minas Geraes. One (Voyage dans le District des Diamans, 135) is near what is now Bello Horizonte, about 10 km. north of Caeté and near the Pico da Piedade, of the view of which St. Hilaire writes with appreciation. This village appears on modern maps simply as Penha. The second (Voyages dans les Provinces de Rio de Janeiro et de Minas Geraes 2: 10) is described as near the settlement of Rio Vermelho in the "termo" of Minas Novas. This Nossa Senhora da Penha is not on modern maps; Rio Vermelho appears about 50 km. east of Diamantina. Since St. Hilaire's label reads "in Mina Nova," it is probably the locality from which his no. *B' 1220* came. St. Hilaire says he found no other place in the province with such varied vegetation.

Brade's drawing, and of Fée's original plate of *N. eriophora* with Hooker's later one.

2. **Notholaena eriophora** Fée, Gen. Fil. 159, *t. 13, fig. 3* (1850–52) and Crypt. Vasc. Brésil 55 (1869); Baker in Mart. Fl. Bras. 1(2): 541 (1870), *excl. t. 66.* PLATE I, FIG. 2.

Notholaena palmatifida Kze. Farnkr. 1: 148 (1844), nomen nudum. Based on *Gardner 2390.*

Polypodium eriophorum (Fée) Hook. Ic. Pl. 10: *t. 991* (1854).

Cheilanthes eriophora (Fée) Mett. Cheil. 23 (1859).

Rhizome 2–3 mm. in diameter; stipe terete, 4–11 cm. long, 0.4–0.5 mm. in diameter; lamina pedate-pinnatifid, 2–3.5 cm. long and as broad or somewhat broader, the basal pair of segments usually much produced on the lower side and strongly inequilateral, their basal divisions on the lower side themselves lobed and somewhat inequilateral, all divisions broadly obtuse; upper part of lamina cut to near rachis into 3–4 oblong, obtuse, entire segments, tapering evenly into a broad, short, 3–4-lobed obtuse apex; texture rather thin, the veins, when indument is removed, visible by transmitted light; ultimate veinlets 1–2-forked, their clavate apices a little back from the margin; indument of both surfaces whitish to rufescent; spores about 42 μ in diameter. — Piauhy and probably elsewhere.

TYPE: Shady clifts on the hills near the city of Oeiras, Piauhy, March, 1839, *Gardner 2390*, presumably at Rio de Janeiro; not seen. Isotypes: BM, G, Gen, K, NY, P, US.

Specimens seen. PIAUHY: Felsenritzen, Serra Branca, Jan., 1907, *Ule 7423* (B); Felsen, Serra do S. Ignacio, Feb., 1907, *Ule 46* (B). State uncertain: Rincas das pedras prope Castro, Jan. 8, 1880, *Schwacke 2545* (B). Without definite locality: *Glaziou 14409* (B, K, P, US); *Herb. Kew. 1037* (Y).

The leads for *N. eriophora* in Brade's key read (translated from the Portuguese): "lamina pedate [i. e. without free pinnae] . . . petioles thinly beset with straight hairs perpendicular to it." Exactly the same secondary lead serves for *N. venusta*. He cites, as cotype (I should have supposed it the type) a specimen of *Gardner 2390*, "ex herb. Fée," sheet no. 30,922 in the herbarium of the Jardim Botanico at Rio de Janeiro, which, of course, he must have seen. Yet his statement is difficult to reconcile with any other evidence.

In the first place, Fée described the stipes in his material as "glaberrimi" — a condition which can readily enough be found in old fronds, the tomentum being deciduous — and they are so figured by him, with the lanate tomentum of the lamina correctly delineated. Hooker figures spreading hairs on the stipes, but his own specimens at Kew, from which his drawing must have been made, show no such thing. Since the tomentum of the lamina is also represented by spreading hairs, one must conclude that Hooker's draughtsman, less accurate and less skilful than Fée's, was merely using a conventional means to indicate any kind of pubescence. All of the nine sheets of *Gardner 2390* which I have seen in various herbaria are alike; all show stipes lanate when young, glabrate in age. This does not, of course, preclude the possibility of a mixture

in Gardner's collection. But in all the material I have examined, I have seen stipes with sparse, spreading hairs only in *N. venusta*, which, of course, can be recognized by other characters. It would seem, if Brade's statement is correct for the type of *N. eriophora*, that Fée must have had a very depauperate individual of *N. venusta*, not sufficiently developed to show free pinnae, and that he misdescribed the stipe — or that there is a sixth endemic in eastern Brazil unknown to me. In any case, suspecting an error somewhere, I am keeping the name *N. eriophora* for the species represented by the nine sheets of *Gardner 2390*.

Phylogenetic conjecture is very likely quite futile in so small and closely knit a group as this; but if it may be permitted, *N. eriophora*, as here understood, is to be regarded as the most primitive of the four pedate species. In it, the leaf-margin is, as Mettenius described it, "omnino immutatus"; at least two of the others (I have not found it in *N. venusta*) have definite, if rudimentary, hyaline margins. The indument is simple, of one type of hairs only, as against two or three in the other species. The sori are borne on only moderately dilated vein-ends appreciably back from the margin. If Bower's opinion is correct — and his cautious and carefully reasoned conclusions deserve all respect — the more or less elongate sorus, borne on scarcely modified veins somewhat back from the margin, is primitive in the Cheilantheae. It is to be hoped he is correct, for, on this basis, one can trace an unbroken and very pretty developmental series from the elongate sorus and unmodified vein-ends of *Pellaea* and some species of *Notholaena*, through short sori, clavate, flabellate and transversely dilated vein-ends, approaching nearer and nearer to the margin, in *Notholaena* and *Cheilanthes*, to the marginal coenosorus and transverse vein of *Doryopteris*. In this series *N. eriophora* would come somewhat between the pellaeoid and cheilanthoid types, belonging, since the sorus itself is short, to the latter, but preserving something of the former. The other species are purely cheilanthoid. *Notholaena goyazensis* might be considered a derivative of *N. eriophora*, and *N. geraniifolia*, with its more complex venation and specialized indument, a still more advanced member of the same line of descent, with *N. venusta* representing a development in a different direction; but there seems little profit in such speculation.

3. **Notholaena goyazensis** Taubert in Bot. Jahrb. 21: 421 (1896). PLATE I, FIG. 3.
Cheilanthes goyazensis (Taubert) Domin in Bibl. Bot. 20: 133 (1915).

Rhizome about 4 mm. in diameter; scales 3–4 mm. long, 0.1–0.2 mm. wide at base, remotely serrulate toward apex, those of the young growth bright brown and concolorous, the older with castaneous, sclerotic central band; stipe 3-10 cm. long, with the tomentum about 1 mm. in diameter, in age glabrate and blackish castaneous; lamina 4.5–6 cm. long, usually about as wide, pinnate-pinnatifid or, in the basal pinnae only, subbipinnatifid, these usually connected with those above by a narrow wing along the rachis, inequilaterally elongate-deltoid, the basal segments on the lower side much produced and pinnatifid with oblong, obtuse lobes;

median segments of lamina linear-oblong, equilateral, pinnatifid with oblong, obtuse, entire lobes, the basal lobes adnate to the rachis and forming a broad, basally narrowed wing along it; the 2–4 upper segments rather abruptly contracted into an obtusish, short or sometimes produced, pinnatifid apex; tomentum of upper surface whitish or grayish, that of the lower surface at first whitish, in age dull brown or pale ferrugineous; margin of the segments with a very narrow hyaline band, scarcely more than one or two cells wide; ultimate veinlets at an acute angle to the costule, simple or once-forked, the fertile ending at the margin of the leaf-tissue in an abruptly dilated, subflabellate tip; spores about 50μ in diameter. — Minas Geraes and Goyaz.

TYPE: Serra Dourada, Goyaz, Jan., 1893, *Ule 3222*, whereabouts unknown.

Specimens seen. MINAS GERAES: São João d'el Rei (Serra de Lenheira), Oct. 13, 1886, *Glaziou 16643* (B, G, K, P); in locis siccis, Serra do Cipó, April, 1905, *Silveira* (P); on rocks in sandstone area, Serra de Bocaina, Municipio de Serro, 10 km. northwest of Serro, May 4, 1945, *L. O. Williams 6871* (G, US). GOYAZ: Entre le village et la Serra dos Crystaes et Caleceira do Rio Samambaia, dans les fissures des roches, Sept. 18, 1895, *Glaziou 22625* (P); Serra de Caraça, May 28, 1907, *Damazio 1859* (B, NY, P, US); without definite locality, *Glaziou 22625* (B, Gen).

As above noted, I failed to find Taubert's type at Berlin. I here use his name in the sense of Christ and Brade, which agrees well enough with the original description. *Ule 531*, from Serra Dourada, Goyaz (P), which I determined in 1937 as *N. eriophora*, may belong here. Christ, who seems to have understood this species accurately, so places it (Bull. Herb. Boiss. II. 2: 381). He was, however, thoroughly confused as to *N. eriophora*. He cited under it Fée's and Hooker's plates, which are *N. eriophora*; *plate 66* of the Flora Brasiliensis, which is *N. geraniifolia*; the collections of St. Hilaire, Schwacke, and Magalhães Gomes here referred to *N. venusta*; and no specimens at all of true *N. eriophora*, as I understand it.

Taubert's name, as here applied, supersedes an unfortunate manuscript name of mine to be found in several herbaria.

4. **Notholaena geraniifolia** St. Hilaire in herb., sp. nov. PLATE I, FIG. 4; PLATE II.

St. Hilarii diagnosis, ipsius manu in schedula scripta, est:

"Stipite gracili, semitereti, subhirsuta: fronde breviuscula profundissime pinnatifida-palmata subtus praecipue hirsutissima: divisionibus angustis pinnatifidis: laciniis breviter linearibus obtusis interdum crenatis — Planta 6–8 pollicaris. Pili paginae inferioris frondis rufi. Stipes atrofuscus."

Quo addendum est sequens. — Rhizoma breviter repens circa 2 mm. diametro, paleis anguste linearibus circa 3–4 mm. longis 0.2 mm. latis medio saturate brunneis subscleroticis, margine angusto hyalino pallido distanter serrulato, apice capillari, dense onustum. Frondes subapproximatae. Stipes quam lamina multo longior (ter vel etiam sexies). Lamina pentagona latitudine longitudinem subaequante; pinnis vel segmentis basalibus inaequaliter deltoideis laciniis basalibus basiscopicis valde elongatis profundeque pinnatifidis, laciniis omnibus plus minusve lobatis; segmentis superioribus laminae circa 4-jugis lineari-oblongis obtusis bipinnatifidis laciniis oblongis vel anguste deltoideis adscendentibus, laciniis basalibus

basiscopicis in rhachem decurrentibus lobos sicut e rhachi exeuntes patentes formantibus; apice laminae brevi pinnatifido obtuso. Pagina superior laminae subdense hirsutula pilis ex comparatione crassis aureo-brunneis nitidis subrectis vix intricatis; pagina inferior lanata pilis aliis gracillimis brevibus densissime intricatis ferrugineis aliis longis subrectis articulatis. Laciniae margine hyalino angustissimo instructae. Venulae 2–3-furcatis, soros breves ad apicem dilatatum parenchymatis margine extremo gerentes. Sporangia in soro singulo pauca breviter stipitata. Sporae subglobosae circa 45 μ diametro laeves vel minute granulatae. — Braziliae in provinciis Minas Geraes et Bahia (?) adhuc lecta.

TYPE: In rupibus prope pagum S. Miguel da Tiquitinhonha, *St. Hilaire B' 1489* in Herb. Paris; seen. Illustration: Mart. Fl. Bras. 1(2): *t. 66* (1870), as *N. eriophora.*

Other specimens seen. MINAS GERAES: Serra de Caraça, Nov. 9, 1913, *A. Maublanc 584* (P); Pantano Agosto, *Glaziou 14408* (B, G, Gen, K, P). BAHIA (?): Auf Felsen bei Calderão, 800 m., Oct., 1906, *Ule 7239* (B).

To this species, clearly distinguishable by the architecture of the blade and the character of the indument, Brade applies the name *N. palmatifida* Kze. This I cannot accept. Kunze mentions the name casually in Farnkr. 1: 148 as that of a species later to be described, with no word of diagnosis, but with the citation of *Gardner 2390* as its sole basis. This is the type-number of the later *N. eriophora* Fée. Kunze's name had been, until Brade took it up, universally regarded as a direct synonym of *N. eriophora*; this still seems the wisest course.

Kunze in 1845 had been chosen to contribute the treatment of the ferns to the Flora Brasiliensis; he no doubt intended to publish this and some other species, of which he spoke similarly, in that work. At the time of his death in 1851 he had prepared fifteen plates for the Flora which were duly published in 1870 by Baker, who took over the treatment of the ferns. *Plate 66*, which, as Brade points out, represents the present species, is one of the fifteen. Baker remarks (p. 541) that the Kunze specimen figured is more deeply cut than those of Gardner figured by Hooker, but gives no hint as to the name which Kunze had originally attached to his plate and seems by his phrasing to imply that Kunze's specimen was not one of Gardner's. There is no direct evidence that it was. It is possible that there was a mixture in *Gardner 2390*, but, as previously noted, the nine sheets of that number which I have seen are alike, and, though confusion of *N. eriophora* and *N. venusta*, or even *N. goyazensis*, might easily occur, it is much less probable in the case of *N. geraniifolia*.

I have nowhere seen any specimen labelled *N. palmatifida* by Kunze. Until the sheet of *Gardner 2390* which he actually had is discovered, existing evidence should be taken at its face value. It is far better and simpler to suppose that Kunze merely gave a name, which he did not live to publish, to the species later described as *N. eriophora* by Fée, and to take up for the present species the indubitable, though not hitherto published, name of St. Hilaire, than to avoid a new name by applying Kunze's in a sense apparently directly contradicted by his citation of type. This is the easier because *N. palmatifida* was never validly published. It began as a

nomen nudum; had, so far as I know, been cited only in synonymy until Brade accepted it in 1940; and was then not provided with the necessary Latin diagnosis.

5. **Notholaena Pohliana** Kze. Farnkr. 1: 45 (1840); Hook. Sp. Fil. 5: 118, *t. 286B* (1864); Baker in Mart. Fl. Bras. 1(2): 541, *t. 48, fig. 3* (1870).
Cheilanthes Pohliana (Kze.) Mett. Cheil. 23 (1859).

Stipe slender, terete, blackish, dull, glabrous or beset with short, pale, retrorse, sometimes branched trichomes; lamina tapering regularly from base to long-attenuate apex, 8–12 cm. long, 2.5–4 cm. wide, with up to 18 pairs of pinnae; rachis like stipe; lower pinnae with 3–5 pairs of free, oblong or deltoid-ovate, obtuse, entire or sometimes lobed pinnules 6 mm. or less long, and a 3–5-lobed deltoid, obtuse terminal segment; rachilla of pinnae black; texture of blades herbaceous, opaque, the veins immersed, 3–4-forked; both surfaces loosely beset with long, simple, distinctly articulate, pale brownish hairs; spores subglobose, about 50 μ in diameter, tuberculate. — Rio de Janeiro, Minas Geraes, and (?) Goyaz.

TYPE (fide Mettenius): Brazil, *Pohl*, perhaps at Vienna; not seen. A specimen of *Gardner 3554* at Geneva, determined by Kunze, may be taken as authentic.

Specimens seen: "Environs de Rio de Janeiro et d'Ouro Preto," 1883–84, *Glaziou 15735* (B, K); Serra da Natividade, Oct., 1839, *Gardner 3554* (B, BM, F as *3551*, Gen, det. by Kunze, K, P, US).

Kunze put forward *N. Pohliana* somewhat casually, as he did *N. palmatifida*, as a species later to be described. In this instance, however, he stated that the new species resembled *N. tenera* in habit, was hairy on both surfaces of the lamina, and had a creeping rootstock. There is only one Brazilian species referable to *Notholaena* which fulfills these conditions; Kunze's statement may therefore be taken as indicating the identity of his plant well enough to constitute technical publication. Mettenius provided a detailed description under *Cheilanthes* and Hooker added a good plate. These agree and with the specimen at Geneva determined by Kunze fix the identity of the species beyond doubt.

There is some question as to the correct numbering of the Gardner collection cited. Mettenius, Hooker, and Baker all give the number as *3551*. Hooker also gives the locality "Serra da Natividade." Yet all the sheets from this locality which I have seen, in seven different herbaria, bear the number *3554*, except one at the Chicago Natural History Museum numbered *3551* and one at Kew (where there are two) in which *3551* has been altered to *3554*. Since all the specimens appear to be of the same collection, I am taking *3554* as correct.

6a. **Notholaena nivea** (Poir.) Desv. var. **oblongata** Griseb. Symb. Fl. Argent. 342 (1879).

Rhizome short, erect, its scales linear or linear-lanceolate, brown, concolorous, with elongate, slender-walled cells; pinnae and pinnules petiolate, the ultimate segments small, oblong and entire or subdeltoid and trilobate, often distant, articulate on their pedicels; sori elongate, occupying at least the outer third of the veins; spores rugose. — Peru, northern Argentina, and Santa Catharina.

TYPE not designated, but said to be from Salta; a specimen at Kew labelled "comm. Grisebach, 1878" is taken as authentic.

Specimens seen: SANTA CATHARINA: San Joaquim, 1000 m., *Spannagel 172* (NY, Pa).

6b. **Notholaena nivea** (Poir.) Desv. var. **flava** Hook. Sp. Fil. 5: 112 (1864).
Notholaena flavens (Sw.) Moore, Ind. Fil. LXX (1857).

Distinguished from the preceding by the characters given in the key. — Colombia along the Andes to northern Argentina; Minas Geraes.

TYPE not designated nor any specimens cited in the original description, but identity clear.

Specimens seen: MINAS GERAES: An Felsen des Campos São Julião, *Schwacke 12764* (P); Miguel Burnier, Preto, *Damazio 1728* (NY, US).

For further discussion and full synonymy of these varieties, see Maxon & Weatherby in Contrib. Gray Herb. 127: 10–15 (1939). Christ, quoting Schwacke, states that var. *flava* is very frequent about São Juliao.

It is not clear whether these isolated Brazilian stations are to be interpreted as the result of migration eastward from the Andes or as relics of once wider ranges. In the Andes all varieties of *N. nivea* are plants of rather high altitudes, descending to lower levels only in the more temperate climate of northern Argentina. The nearest known stations are in eastern Bolivia and in the province of Córdoba in Argentina; they are some 800 miles from the Brazilian locality in Santa Catharina and some 1200 from Minas Geraes.[4] It is possible to postulate a migration-route from eastern Bolivia across the upper Paraná basin, where the gap between the Bolivian and Brazilian highlands narrows to 250 miles, but, pending the discovery of intermediate stations, this must remain pure conjecture.

[4] The two stations in Minas Geraes are close together, perhaps the same.

EXPLANATION OF PLATES

PLATE I

The drawings are intended to show outline of blade and venation; in all cases, indument and sporangia are removed. Blades are approximately × 1; single pinnae or segments, × 3; fig. 3c, × 6.

FIG. 1. *N. venusta:* a, outline of blade from photograph of *St. Hilaire B' 1220,* type of *N. capillus*; b, median pinna from *Schwacke 14520.* FIG. 2. *N. eriophora:* a, outline of blade, from photograph of a sheet of *Gardner 2390* at Kew; b, median segment from sheet of *Gardner 2390* at Herb. Gray. FIG. 3. *N. goyazensis:* a, outline of blade; b, median segment; c, two lobes of the same; all from *L. O. Williams 6871.* FIG. 4. *N. geraniifolia*: a, outline of blade; b, median segment; both from *Glaziou 14408.*

PLATE II

Type of *N. geraniifolia, St. Hilaire B' 1489* in Herb. Paris.

GRAY HERBARIUM,
HARVARD UNIVERSITY.

"Notholaena" in Brazil

"Notholaena" in Brazil

MORE PLANT STUDY: FEWER PLANT NAMES

Carleton R. Ball

Nature produces infinite variety. Man (the taxonomist) desires, imagines, and describes uniformity. Therein lies perpetual confusion and conflict. Before obvious differences can be evaluated, we need to understand their nature, extent, and probable causes. The writer can speak definitely only of the genus *Salix* (willows).

FOUR MAJOR CLASSES AND CAUSES OF VARIATION

Four major classes of variation occur normally on shrubby and/or arborescent willows, and to a lesser degree on prostrate and creeping species. A: The same organ, on one part or on different parts of a single plant, normally presents striking variations. The pattern is permanent but the expression is modified by environmental conditions. B: An individual organ usually or often shows great variation during the course of a season or a year. These variations are the direct result of the advance from spring to summer, to autumn, and back to spring again, but their expression will be modified by differing conditions in differing seasons or years. C: Plants of a single species, growing under obviously different conditions of local environment, frequently present large variations from spot to spot. While presumably environmental effects, these variations may include the hereditary differences of Class D also. D: Two or more individuals, growing under apparently identical conditions of local environment, frequently display obvious differences. These should be hereditary variations, if the environments actually are identical, but are influenced somewhat by the age of the plant.

A. Variation of an Organ on a Single Plant

The Individual Leaf. As the leaf emerges from the bud-scale, the outer or apical portion broadens first. This broadening progresses toward the base. If the nutrient supply is reduced by competition farther out, before growth of the leaf is completed, the lower (first developed) leaves may never finish normal basal expansion. Leaf-bases may remain cuneate, acute, or rounded, which should have become acute, rounded, or cordate, respectively. The tip also may fail to elongate, leaving the apex obtuse or acutish when it should have been acute or acuminate.

Different Leaf Forms on a Single Twig. On any given twig, there will be three successive and intergrading sizes and shapes of leaves, occupying basal, central, and apical locations on the twig. The basal leaves in general will be smaller, narrower at base, and broader and blunter at apex than the

central leaves. The apical leaves will tend to be larger, broader at base, and more acute or acuminate at apex than the central leaves. The central leaves, therefore, are somewhat intermediate between the basal and apical leaves in size and shape, just as they are intermediate in position and time of development. In general, therefore, there is a steady progression in leaf size and shape from the base (first developed) to the apex (last developed) of the twig. This progression tends to recapitulate the developmental history of the individual leaf. These facts hold, no matter what the normal shape of the leaf may be.

Four Types of Twig Per Plant. Normally there are three, and sometimes four, types of leafy twigs produced successively during each season. Type *a* is represented by the short twigs which develop simultaneously with the fruits, from lateral leaf-buds on the fruiting twigs. Type *b* is represented by the longer and somewhat vigorous twigs which develop, after fruiting is over, from apical buds on the fruiting twigs. Type *c* is represented by the vigorous shoots which develop later from buds on older wood, after the food-drain of fruiting is over. Type *d* is represented by the luxuriant shoots (water sprouts) which sometimes develop on trunks and/or roots in late summer. Schneider (10, p. 9–10)[1] discussed parts of this problem briefly in 1918, but in somewhat vague language; the writer (4) more fully in 1943.

On each of these four successive types and sizes of branchlets, there will tend to be the same progressive shift in size and shape of leaves, from base to apex, as was described above. But in addition to this normal progression, all the leaves on type *a* tend to be shorter and relatively broader, all those on type *b* tend to be intermediate, and all those on type *c* tend to be larger than on the others. These changes, like those on a single twig, probably represent the more abundant food supply and more favorable temperatures as the season advances. Fruiting limits nutrients available to early shoots and rapid elongation of a summer twig may cause food to bypass the basal leaves. Sometimes the apical leaves on late-produced type *c* twigs do not attain full size because of drought or cold in autumn. The leaves of all three groups on the sprouts of type *d* often are enormous in size and more or less different in shape, but there will be the same general progression from base to apex of sprout. Because of the variations just discussed, the writer often takes from three to six or seven sheets from a single plant.

B. Variation of an Individual Organ During the Year

Twig, Bud-scale, and Branchlet Changes. These organs, as well as petioles, may change greatly in color and clothing during the successive seasons of a year, and the twigs during successive years, as they become 1-year and 2-year branchlets. These changes are caused by plant reactions

[1] Numbers in parentheses refer to "Literature Cited" at end of paper.

to sun, temperature, rain, etc. In general, they are greatest in plants in full sun and on those organs in direct sunlight.

In general, colors darken as the season advances. Original yellows, light greens, and light browns become varying shades of darker brown to blackish. As new twigs are produced during the summer, each must pass through these changes. In a few species, as *S. amygdaloides* and *S. lutea,* the yellow is permanent. In parts of Alaska and Yukon, as noted by Dr. Setchell, the abundant *Salix Barclayi* colors the spring landscape with its bright yellow twigs and the very light yellowish green of the unfolding leaves. But in the herbarium, and the manuals, the branchlets are blackish. The occasional bits of still-yellow epidermis are neither large enough nor numerous enough to be conspicuous. The same facts are true of *S. monticola* in the Rocky Mountains, according to the continuing observations of Professor Ernest C. Smith. After going through the press, the twigs, with rare exceptions, are like those of *S. Barclayi.* By extremely careful drying, much of the yellow color may be retained.

Twig, bud-scale, and branchlet hairiness is one of the most variable characters of the vegetative organs of willows, and presumably of other plants as well. It is highly external, being a product of the epidermal cells and therefore greatly influenced by temperature, sun, etc. Its primary function probably is protection of young tissues against sun scald. In many species, the seasonal shoots (hornotini) are more or less densely puberulent, pubescent, or tomentose. This covering may be present in lesser degree as these shoots become 1-year (annotini) and 2-year branchlets in succeeding years. In other species, the seasonal twigs may be completely glabrous and remain so in later years. All this sounds simple, but. . . .

The conspicuous pubescence of a new shoot may wear off gradually during autumn and winter, leaving glabrate to glabrous twigs in spring. Many species shed the epidermis from the branchlets in spring or early summer and, of course, the hairs go with it. In such cases, there usually are "armpit" areas on the twig, behind buds or lateral twigs, where the epidermis was not deciduous and tell-tale remnant pubescence may be found. Hairiness of bud-scales usually parallels that of twigs.

Twig and bud-scale pruinosity occurs on such species as the western *S. irrorata, S. Lemmoni,* and *S. subcoerulea,* the northeastern *S. pellita,* and the European *S. daphnoides.* This waxy exudate is more external and less stable than the wax causing glaucousness of leaves, and therefore is more temporary in nature. It may be washed off by rain or snow, gradually removed by slow weathering, or completely discarded with peeling epidermis (5). Many other species, northern and arctic, occasionally show some pruinosity of bud-scales, branchlets, or even capsules, with organ frequency in the order named. This has little diagnostic value, because of infrequent and irregular occurrence, confinement to a small part of the eligible organ surface, or quantity so dilute as to be distinguished only with difficulty.

Leaf Structure. Leaves and stipules may change greatly in degree of gland-presence, serration, and vein-prominence during the season, as they develop from juvenile to full-sized, to mature, and to senescent condition. Glands may drop off and serratures may enlarge. Many species have normally entire leaves but scarcely one of these will fail to show some serration on vigorous apical leaves. Venation often becomes increasingly prominent with age in some species, under conditions little understood. Unusual specimens become varieties or forms under such names as *venulosa, marginata, reticulata,* etc.

Leaf Hairiness. The leaves of many, probably most, species of willows are more or less hairy, on one or both surfaces, while they are unfolding. If densely hairy at first, they become less so through expansion of area, even if no hairs drop off. For those kinds not permanently hairy, the rate of hair fall varies with the kind, the environment, and the individual, just as in the human races. Those which have a natal coating of very long hairs on the under-surface usually lose them quickly (*S. anglorum, S. laevigata*), and persistence is greatest at the tip. Those with shorter hairs are likely to lose them more slowly, first from the leaf-surface, then successively from the larger veins and outer midrib, and finally, if at all, from the lower midrib and petiole. Some arctic species remain ciliate on the margins. Species with permanently hairy leaves are found more commonly in cool and cold climates than in dry and hot areas, but there are exceptions. The hairs normally become thinner with age and some individuals in nearly all species lose most or all of the hairs by autumn. From this, we have varieties and forms named "glabra," "glabrescens," "tonsa," etc. How about naming balding humans?

Leaf Glaucousness. The glaucescence or glaucosity of the lower surface of the leaves of many species of *Salix* are valuable and usable taxonomic characters, if botanists understand the chemistry and physiology of this expression. It is the result of a waxy secretion, and the time of appearance and quantity produced seem to be governed by physiological processes. In species which normally are heavily glaucous, the whitening of the under-surface is apparent when the leaves begin to unfold, as in *S. longipes, S. laevigata, S. discolor,* etc. In species normally less densely glaucous, the color may not become visible until the leaves are half-grown, as in *S. cordata* and some relatives, *S. sericea, S. lasiolepis,* etc. In still others, as in the western *S. lasiandra* and the introduced *S. fragilis,* the under-surface may remain pale green until the leaves are full-sized.

To add to taxonomic troubles, this white waxy substance is destroyed by too rapid or too hot drying of fresh specimens. This occurs often when electric driers are used. The glaucous condition cannot be restored. The blades remain permanently "green on both sides" and cannot be identified by the usual keys.

Floral Organs, such as aments, peduncles with their bracts or leaves, flower-scales, glands, stamens, and capsules with their pedicels and styles

and stigmas, likewise change greatly as they develop from the juvenile stage to maturity. Not only this, but the relative lengths of any two organs may change because some start earlier, or elongate faster, or continue growth longer than others. Some of those maturing quickest (glands, styles, and stigmas) may even shrink after maturing and so change relative dimensions. Yet some recent taxonomists still describe floral organs in terms of relative lengths, without regard to the degree of maturity of the two organs compared, as "gland equalling the pedicel," "styles ½ as long as pedicel," or "scale twice as long as the gland," etc. Such statements often are wholly misleading for taxonomic purposes.

There often is 100 percent variation in length of floral organs (except capsules) in a single ament, and it is not regular and progressive from base to apex or the reverse, although pedicels and scales tend to be longest at the base of aments. Scales are especially puzzling, as they usually are relatively short and broad in the opening ament and there is relatively little uniformity at maturity.

Scale Color and Hairiness. Scales in several Sections of *Salix* are pale yellow and deciduous. They may become pale brown in weathering or drying. In two Sections (*Glaucae, Rostratae*) with persistent scales, these are yellowish or light brown and may weather or dry to a medium brown, especially at the normally visible apex. In other Sections, the scales usually are dark brown to black and remain so, although light brown scales occur occasionally.

Flower-scales of most willows normally are hairy, primarily for insulation and protection of the subtended organs. In most species, these hairs tend to drop off gradually, especially from the outer surface. Some scales become glabrate outside, others remain hairy. Some northern and arctic species, however, have scales glabrate or glabrous from the beginning (*S. pyrifolia, S. leiolepis, S. chlorolepis*).

Capsule Hairiness. Many species have permanently hairy capsules and almost never is a plant found whose capsules have become entirely glabrous in age. Only rarely do these species have varieties with normally glabrous capsules. Exceptions are *S. brachycarpa* var. *glabellicarpa;* also the species *S. chlorolepis.* In Sections *Commutatae* and *Chrysanthae,* having some species with permanently hairy capsules and other species with normally glabrous capsules, the latter species are likely to have varieties with more or less hairy capsules (*S. Barclayi* var. *hebecarpa, S. commutata* var. *puberula, S. Hookeriana* var. *tomentosa*). Hairy-capsuled species in these sections do not have glabrous-capsuled variations. In some Sections (*Nigrae*) with normally glabrous capsules, variations with pubescent capsules may occur (*S. Gooddingii, S. Humboldtiana* var. *Martiana*), but the hairs usually are deciduous before capsule maturity.

C. Plant Variations Caused by Differing Local Environments

Every farmer and farm boy know the difference in height and color of

maize plants in different parts of a single rolling clayey field: stunted and yellow plants on the dry and stony hilltops, because of lack of water and food; normal green and healthy plants on the lower slopes because of more water and sufficient fertility; deep green and luxuriant plants on the flat, fertile, well-watered bottoms, through exceptionally favorable conditions; marked differences in the size and color of plants and all of their organs. Yet all grew from the same lot of seed, in the same season. The ear-size of all three groups will be proportional to plant-size, but the hereditary characters, kernel-row number and kernel shape and color, will not be changed by these local influences.

Wild plants respond in the same way to moisture and fertility differences in rich, well-watered alluvium, drier second-bench, sterile sand or gravel bars or sand dunes, and dry and barren hilltops, wherever the same species gains a foothold in several or all of these habitats. In the drier and more sterile locations, the plants will be depauperate and the vegetative and many of the floral organs will be reduced accordingly. In the average or normal habitats, the plants will be normal and their organs will tend to be of average dimensions. Where moisture and fertility are high and temperatures favorable, as on a mid-latitude alluvial flood-plain, the plants will be luxuriant and their organs will respond by tending to reach sizes well beyond the normal. But these differences, however striking the extremes, do not make the different plants into "new" species or varieties. They should be labelled for what they obviously are: "depauperate," "normal," and "luxuriant." If conditions were changed, the plants would change also.

Conditions producing extreme heat locally may result in striking changes in affected plants, such as depauperate growth of plant and parts, extreme hairiness, etc. Such conditions occur on sandy and rocky situations, as bars, blow-outs, dunes, quarries, out-crops, etc., where extreme radiation of heat may occur. In the same way, extreme shade may cause remarkable differences in size, shape, thickness, and color of vegetative organs.

When the leaves of certain species of willows (*Longifoliae*) are eaten off in summer by sawfly larvas, a full new crop of much smaller leaves is likely to appear. They usually will be densely white-hairy, probably a reaction to midsummer temperatures much higher than those prevailing when leaves normally are unfolding. These plants are very deceptive in appearance, looking like something very different from what they really are. Usually, however, some attached fragments of the original and much different leaves may be found and the deception unmasked.

D. Actual Hereditary Differences

We see differences between individuals of the same species, even when growing under apparently identical conditions. If the conditions actually are identical, then these differences should be real and hereditary. The number of such differences, the regularity of their association, the uni-

formity of their expression, and the degree of their departure from the norm of the species will be factors in determining whether any of the plants warrant recognition as different taxonomic entities.

These basic facts can be verified only by a study of numerous plants in the field, in different geographic areas of the species range. Having in mind, however, the above-presented facts regarding variations, much may be deduced from a study of abundant and widely collected herbarium material. In the case of shrubby and arborescent plants, a herbarium specimen is but a fragment at best. Because, in *Salix* for example, the two sexes are on separate plants, it is a fragment of only one half. A series of specimens, unless specially collected, is only a series of fragments of the halves. And even if an extensive series came from plants which were practically identical, they would have been collected at different times in the season, at different periods of development, and from different portions (expressions) of the plants. And no two plants *are* practically identical. Some will be undeveloped or juvenile, other full-sized, still others mature. Unless the whole series is quite extensive, therefore, no satisfactory large-scale comparison is possible.

Furthermore, the average herbarium labels carry few or none of the data which might enable the taxonomist to determine if local environments (habitats) actually were similar, let alone identical. For these reasons, the student cannot be completely sure whether the differences observed on specimens are actual and hereditary or the effects of local environmental influences, either permanently or temporarily prevailing. To name new species or varieties, therefore, from one or a few fragmentary specimens under such conditions is to shun personal responsibility and to leave the real labor for another to perform later.

COMBINING PRECEPT AND EXAMPLE

Precept is easy and often abundant. Example is difficult and often proportionately rare. Certain important precepts have been set forth above. Summarized, they read: "Know what to expect from plants growing under different conditions, and why."

Below are outlined two quite different methods of studying botanical material for taxonomic purposes. In either case, it is assumed that the material represents, or is supposed to represent, a given species and its varieties, together with closely related species of possibly doubtful validity, and species and/or varieties currently held to be synonyms.

Two Methods of Studying Taxonomic Material

The first method is to obtain the largest possible collection of specimens representing all of these real, supposed, and/or unadmitted entities. Better still, study large numbers of living plants in the field, in different habitats in various geographic areas of the total range. Even better yet, do both. Because adequate field study is difficult or impossible for many students,

chief dependence must be put on herbarium material. In any case, the specimens should be sorted out by geographic areas, without regard to the names which have been applied to them previously. Whether living or dead, complete or fragmentary, they are studied critically for similarities and differences, and the differences are analyzed as to nature, causation, and value, on the basis of the previous precepts. All this is without cross-reference to the previously published descriptions of the species and varieties involved.

This is the centripetal method, working from the outside in. It gets to the heart of the matter. It assumes the possibility of specific unity of the material. It challenges the mind to discover if there are differences, and to prove whether discovered differences are inherent or merely the effects of local environment. It says: "Find out what there is, — then what others thought there was." It keeps the mind free from prejudice while this is being done.

The second method is to study, successively, the descriptions and the cited or supposed material of each of the named species and varieties known or suspected to belong within the broad limits set. When one such has been studied and segregated, another is taken up, and so on until all have been covered. This is the centrifugal method, working from the inside out. It flies out from the center in all directions. It assumes differences, consciously or unconsciously, because others have done so. One is following a blazed trail instead of blazing one. Others have applied different names, have emphasized different characters or appearances, and have made comparisons to prove that significant differences exist. There is an internal pressure to verify what others have found or decided. All of this influence is present in addition to the urge to father more entities, new or resurrected, especially just before a new edition of a manual.

Standards for Taxonomic Workers

At present there are no professional standards or requirements for taxonomic workers. Each is a law unto himself, although their products affect tens of thousands of students and teachers, either as a help or as a burden. This lack of standards is responsible in part for the lack of respect in which this profession is held. If embryo taxonomists were required to go out and measure and record the range of variation in organs on a single large living plant or on numerous smaller plants of several species, they would return both tired and amazed. If they were required to follow the progressive variation of all organs on a plant through all of the seasons of even a single year, they would become both enlightened and humbled. Knowledge, with amazement and humility, is an excellent foundation for future taxonomists.

Such procedure would insure fuller and more accurate descriptions of plants, in journals and in manuals. With that, more people would know more about more plants. It also would curb the present tendency to

consider every observed variation as a novelty to be named. This would mean reduction in the flood of synonyms, so expensive of time and money. It would keep systematic botany simpler and taxonomists more respected. The end result would be more time and money spent on knowledge of plants and less on knowledge of names. Many years ago, when a great university inaugurated a program of "humanizing instruction at the freshman level," a non-botanist said to the president: "I have seen a miracle on this campus." "What have you seen?" he was asked. "I have seen a class in botany out of doors looking at a plant," was the reply.

Many new species and varieties have been based on these major developmental and environmental variations. This will continue unless there is better teaching. Even a single leaf from each of the three series on a single twig, or three from each of the four twig-types on a single plant, may become the type of supposed new entities. A paleobotanist may do just that because, to him, a leaf is a determinable and usable unit. If two or more leaves are markedly different, they must represent, of course, different entities. Let us use a little common sense in this matter of basing novelties on such variations. Let us not make another 1000 so-called species of *Crataegus*, or of any other genus, with the type specimens of three species taken from one tree.

All are familiar with the often striking differences between the children of the same human parents. All had exactly the same ancestors, but some are short and some tall, some slender and some stout, some fair and some dark, and some quick and some slow. But we do not insist on naming new varieties and forms based on these differences. Nor do we base new species on the differences between the juvenile and the adult human organism.

Example: Exit Salix missouriensis Bebb

Turning now from precept to example, there is set forth an example of the results obtained when variable taxonomic material is studied by the centripetal method. Some may not agree with the conclusions reached. Conclusions in taxonomy always must rest on personal judgments. But it is hoped that there may be agreement as to the value of the method used.

In 1867, Andersson (2, p. 159), the Swedish salicologist, in a monographic discussion of *S. cordata* Muhl., arranged *S. rigida* Muhl. as a subspecies and thereunder created a new variety, *vestita*. This was based on a single juvenile specimen collected by Neuwied at Ft. Osage on the Missouri River (not far from present Kansas City). Of it, Andersson says: ramis crassiusculis, annotinis tomentosis; foliis novellis plus minus dense sericeo-tomentosis, lucidis, integris; amentis ♀ crassis praecocibus omnino nudis, rachi dense villosa, squamis sat longe pilosis, capsulis e basi sat crassa conicis stylo haud elongato apiculatis."

In 1868, Andersson (3, p. 252) presented var. *vestita* again, this time as a seventh variety of subspecies *rigida*. The description is shortened and

the reference to thick branchlets omitted. The plant would pass for *S. cordata,* except perhaps for the stout aments and the long-haired scales.

In 1895, Bebb (6, p. 373) decided to raise Andersson's variety to specific rank but, because of the earlier *S. vestita* Pursh, he named it *S. missouriensis* and designated it as "n. sp." Needed parts of his long description will be given in the discussion of plant and organs which follows. He was somewhat doubtful of the validity of his species, however, and said:

> "For one of the Cordatae, the extraordinary height and size of trunk attained by this Willow, the repeated [reputed?] durability of the wood for fence-posts, its early period of flowering, together with the technical characters above given, would seem to amply warrant its elevation to the rank of a valid species. At all events, as such, it is more likely to receive that further study and criticism which will determine its true status, than if left as a doubtful variety within the limits of such a polymorphous species as S. cordata."

Several items in Bebb's description and discussion require comment. If the comments appear derogatory of his judgment, let us remember that he always had been careful and conservative, that here he apparently was grossly misled by others on two important points, and that he was aged and failing (he died in 1896).

In the past six years, the writer has studied more than 1000 sheets of *S. cordata* and *S. missouriensis* in his own herbarium, the U. S. National Herbarium, and that of the University of Nebraska. Increasing Nebraska collections by Dr. Walter Kiener soon convinced him that *S. missouriensis* was not a distinct species but at most only a variety (var. *vestita* Anderss.). Since the preparation of the above discussion of the nature and causes of variation, and the appearance of Dr. Fernald's recent discussion (7, p. 27–28) in Rhodora, most of this material has been reviewed for data on the points at issue, with the further conclusion that var. *vestita* is not even a valid variety, for the reasons given below.

Polymorphism. Bebb refers to *S. cordata* Muhl. as polymorphous. It is. All willows (and other plants) are, although perhaps not in just the sense Bebb meant. That polymorphism is the thesis of the present paper. *S. cordata* is an excellent illustration of the principles set forth herein. It has a range (with var. *vestita*) of almost 2000 miles east-west and some 1100 miles north-south, with a corresponding diversity of climate, soils, and local habitats. It is a large enough shrub to permit expression of the maximum variation on a single plant.

Height and Diameter. Bebb describes his species as a tree "thirty or forty, or even fifty, feet in height, trunk ten or twelve, rarely eighteen inches in diameter." Sargent, in 1896 (9, p. 137), repeated these dimensions and later manuals have repeated the height. Where did Bebb get this record of tree-like height for a shrubby or arborescent plant? He had never seen it growing, but refers to collections by Sargent and Bush from Courtney, Jackson Co., Mo. There are three true tree willows which

occur along the Missouri in that area, namely, *S. longipes* (var. *Wardii*), *S. amygdaloides*, and *S. nigra*. All three may attain the height, and rarely the trunk diameter, recorded by Bebb. It seems almost certain that, if Sargent or Bush furnished the height data, they included plants of one or more of these tree species when estimating maximum height and diameter. *Salix longipes*, especially, bears a deceptive resemblance to luxuriant *S. cordata* (var. *vestita*).

Most collectors do not record heights of plants collected. In the Bebb Herbarium at the Chicago Natural History Museum are three specimens collected by Bush in 1892 along the Missouri River in Jackson Co., Mo. It may be that Bebb's species was based on these, but no heights are given on the labels. One is said to be a tree 12 inches in diameter and two are called small trees, with 10- and 6-inch diameters, respectively. In 1895 and 1896, Dr. Glatfelter collected at least 31 specimens of var. *vestita* (distributed as *S. cordata* × *S. sericea*) in and around St. Louis, Mo., the labels giving heights and often diameters. Of these 31, only ten reached 20 ft. or more. Three of these ten reached 25 ft., with diameters of 5.5–7 inches. Only one was 30 ft. high, with 7-inch diameter. These taller plants mostly had single stems, dividing low. Other collectors record heights from 15 to a maximum (Ia.) of 27 feet. It may be that Sargent was responsible for the exaggerated height record. In any case, the Jackson Co. plants were from conditions of moisture, fertility, and climate which make all vegetation remarkably luxuriant. The eastern plant has a general height of 10 to 20 feet, with the maximum somewhat more.

Branchlet Size and Hairiness. In 1867, Andersson (2) described very stout twigs, but in 1868 he dropped the phrase. Bebb said: "one-year-old twigs stout." Actually, twigs show just about the same stoutness from the Great Plains to the Atlantic.

Hairiness varies in exactly the same ways throughout the entire area. It is fixed in many minds that the vegetative parts of *S. cordata* are glabrate or glabrous and those of var. *vestita* are hairy. The study of some 1000 specimens shows hairiness (puberulence, pubescence, and/or tomentum) to be practically universal. The white-pubescent seasonal twigs occur in Lower Canada, New England, the Potomac-Shenandoah Valleys, the Appalachians, and the Lake States, as well as in the Mississippi-Missouri Valleys. The denser the twig pubescence, the more frequently it is associated with pubescence or bud-scales, petioles, midribs, and sometimes stipules and young blades. Glabrate to glabrous yellowish seasonal or 1-year twigs were more common westward in the drier areas, but many 1-year and 2-year twigs glabrous in spring showed tell-tale remnant pubescence behind buds and lateral twigs. The long season and high summer temperatures of the lower Missouri are favorable to denser pubescence of twigs.

Leaves. Andersson's type had only very young leaves. Bebb describes the leaves as:

"... lanceolate or oblanceolate, five to six inches long, from one to one and a half inches wide, cuspidate-acuminate, narrowed from above the middle toward the acute or rounded (but not truncate or cordate) base, at first more or less clothed with silky hairs, soon smooth and dark green above, except the downy midrib paler, but not glaucous beneath, margin glandular-serrate; petioles downy, half an inch long, ..."

These statements regarding leaf-length, leaf-base, and glaucousness are not true for either the western or eastern plants. The leaves of "*S. missouriensis*" by no means average 5–6 inches long. On fruiting twigs and many early seasonal twigs, the leaves are 3–4 inches long and 0.7–1 inch wide. On more vigorous seasonal shoots, they reach 5–6 inches long by 1–1.5 or 1.8 inches wide.

In the eastern area, the leaves average about the same in size, on comparable twigs, as in the western. Relatively large leaves, up to 5.5 inches long and 1.4–1.7 inches wide, are found frequently from Lower Canada and New England southward. Westward, the leaves tend to average narrower. One specimen from Maine has blades 6.5 by 1.4 inches, while specimens from Quebec, Vermont, and New York run to 6 by 1.5–1.7 inches. Petioles on leaves in the Northeast range from 0.5–1 inch long. In Virginia, leaves range up to 6 by 1.75 inches; in West Virginia to 5 by 1.5 inches. None larger have been found in the Missouri River area, on either supposed species. Specimens with shorter but relatively broad leaves occur sparingly throughout and are likely to be associated with densely pubescent shoots, bud-scales, petioles, midribs, and sometimes blades.

In the material assigned to *S. missouriensis,* the bases of the larger leaves commonly are truncate and some are strongly cordate (*Glatfelter 13*), Bebb's note to the contrary notwithstanding. The range for leaf-base shape is exactly that for accepted *S. cordata.* In both eastern and western plants, mature leaves are glaucescent to glaucous beneath, although the color may not develop until the leaves are nearly full-sized. The leaves on autumnal collections of both plants usually are strongly glaucous.

Early Flowering. One of the distinctive characters asserted for *S. missouriensis* was its early flowering. Bebb quotes Bush as follows: "The aments usually open about the first of February and have passed out of bloom by March 1st, whereas those of Salix cordata do not appear till the first week in April." This is a difference of about two months, if true, but it does not happen to be true. Let Bush's own collections speak. In 1896, he collected *S. missouriensis,* nos. *448, 464, 470, 475,* and *480,* at Courtney, Jackson Co., Mo., between April 11 and 19, the first spring after Bebb's publication. These five specimens, in U.S. Nat. Herb., bear just-opening aments, not-yet-flowering aments, flowering aments, and young fruiting aments, all 10 weeks after flowering should have started and 6 weeks after it should have ended, according to Bush. This was not confined to 1896. Number *6552* has 3-inch pistillate aments in flower on April 15, 1912, as delayed as those of 1896. Number *7719* has sessile 2-inch aments in flower on March 24, 1916, seven weeks after it should have begun and 3

weeks after it should have ended. The Glatfelter specimens from St. Louis were in bud from March 25 to April 7; in flower from March 27 to April 12; and in young fruit from April 17 to 24.

Ament Length and Laxity. Bebb described the aments as precocious, sessile, dense-flowered, the staminate oblong, 1.5–2 in. long by 0.5 in. wide, the pistillate lengthening to 3 in. and becoming more or less lax in fruit. Sargent (9, p. 137), in 1896, adds another inch gratuitously ("3–4 inches long"). The maximum (not average) is 3 inches. Abundant material shows that the pistillate, at flowering, are 1–2 in. long, lax, borne on short (0.5 cm.) bracted peduncles. In fruit, the aments become 1.5–2.5 or rarely 3 inches long (*Bush 6552*) and very lax, and the peduncles become up to 1 cm. long, with small leaves. Laxity is a function of rachis and/or pedicel elongation. The pedicels become 1.5–2.5 or rarely 3 (*Bush 475*) mm. long, the capsules 6–7 mm. and the styles 0.5–0.6 mm. long. Eastern material shows aments up to 2.5 inches long from Lower Canada, Massachusetts, and New York, and one Massachusetts specimen (*Forbes 563*) has aments up to 3 in. (7 cm.) long. Pedicels up to 2–2.5 mm. are frequent in the east and 3-mm. pedicels occur in New Hampshire (*Rand & Robinson 652*) and Massachusetts (the Forbes plant with 7-cm. aments).

Scale Length and Hairiness. Both Andersson and Bebb stress the length of the flower-scales and of their densely investing hairs. Both were studying specimens from luxuriant plants whereon most organs were larger than average. Also, the resulting ament laxity enabled the usually partly hidden scales to be easily seen. These facts are true also of luxuriant plants in the eastern area.

Capsule Length. Neither Andersson, in describing var. *vestita,* nor Bebb, in creating *S. missouriensis,* mentions capsule length, so apparently they saw no difference from that of *S. cordata*. *Salix eriocephala* Michx., which Fernald says is the same as *S. missouriensis* Bebb, is staminate. Andersson completely misinterpreted *S. eriocephala* from beginning to end (1, 2, 3), so that his statements about capsules obviously apply to those of other species. Fernald (7, p. 27), however, says: ". . . , the very large precocious aments and long (up to 1 cm.) capsules having deceived those who did not consider the other characters, . . ." Fernald gives no authority for this assertion of unprecedented capsule length, an increase of some 43% over the maximum recorded.

Measuring the capsules on numerous luxuriant specimens from the Missouri flood-plains, the normal length is found to be 5–6.5 mm., with a few reaching a maximum of 7 mm. long. Outside the most favorable habitats, the capsules also average 5–6.5 mm. but never reach 7 mm., so far as seen. The capsules of accepted *S. cordata* normally run to 6 mm. long and occasionally to 6.3 mm.

Summary of "S. missouriensis." The great height and diameter ascribed are not proved and remain extremely doubtful. The tomentum of twigs is shared by many eastern specimens, although Missouri-Mississippi Valley

conditions are conducive to extreme hairiness. Long leaves and truncate to cordate bases occur throughout the entire area. The reported extremely early flowering is disproved by the records. Expanded pistillate aments are not sessile and naked. The long aments, scales, scale hairs, and pedicels are matched by those on equally luxuriant eastern specimens. The long capsules asserted by Fernald just cannot be found on any plants. *"Salix missouriensis"* is merely the luxuriant expression of *S. cordata* Muhl. under favorable conditions of temperature, moisture, and fertility.

"Accurate and Cautious Salicologists." Fernald (7, p. 29) designates the Swedish salicologist, N. J. Andersson, as "the most accurate student ever to work on *Salix*, . . ." He further said (7, p. 31) ". . . it is . . . the highest of honors to get near the limited group of most cautious salicologists with Nils Johan Andersson!" Let us consider just what Andersson did with *S. eriocephala* Michx. and *S. cordata* var. *vestita* Andersson, which Fernald states to be one and the same (Section *Cordatae*).

In 1858, Andersson (1, p. 117) placed *S. eriocephala* in a group with *S. lasiolepis* and its relatives (*S. Bigelovii, S. irrorata*), all of Section *Lasiolepes* (related to *Cordatae*), and threw in his wholly unrelated *S. Coulteri* (closest to *S. sitchensis,* Section *Sitchenses*) for good measure. *Salix cordata* is not mentioned. In 1867 (2, p. 85) and 1868 (3, p. 225), he arranged *S. eriocephala* as a variety of *S. discolor* (Section *Discolores*), even more distantly related than *S. Coulteri.* In all three papers, his extended discussion contains repeated expressions of uncertainty and repeated comparisons with many and diverse species, but always with *S. discolor* and its relatives, to which it is least related.

In 1867, Andersson (2, p. 159) created his hairy-twigged var. *vestita,* specifically identical with *S. eriocephala* (fide Fernald), and assigned it to *S. cordata,* even noting its glabrous capsules. But he compared it with *S. discolor,* which has glabrous twigs and pubescent capsules with quite different styles and stigmas. This treatment was repeated in 1868 (3, p. 252), without the reference to *S. discolor.*

Andersson, in short, dealt with two specimens of an identical entity, collected in the fertile flood-plain within 400 miles of each other. The pistillate he made a variety of *S. cordata,* where it belonged, but compared it with the unrelated *S. discolor* in spite of its hairy twigs and glabrous capsules, the opposite of *S. discolor.* The staminate plant he first assigned to the *Lasiolepes,* close to *Cordatae,* but then shifted it to *S. discolor,* a completely unrelated species, and invented a pistillate plant to justify that disposition.

Many similar acts by Andersson have been cited by Bebb and others and many more remain uncited. When Fernald assigned to the capsules of *S. eriocephala* a length of 1 cm., he perhaps achieved a certain nearness to Andersson in accuracy and caution.

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TYPES OF SOME AMERICAN TREES

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With three plates

Quercus velutina Lam. Dict. 1: 721(1783) or *Q. tinctoria* Bartr. ex Michx. Hist. Chênes Am. no. 13, *tt. 24* and *25*(1801), at least as to *t. 25*, is, as Sargent said in his Man. Trees N. Am. 239(1905), "more variable in the form of its leaves than the other North American Black Oaks," though its cups, with their grayish-pubescent and thin, free-tipped and acuminate scales, quickly distinguish it, as do the large tomentose winter-buds and the deep yellow or orange inner bark, which gave it the once familiar name, Quercitron. In fact, the foliage, which is remarkably constant on individual adult trees or colonies but discouragingly different on trees of some other colonies, inspired the godfather of the Arnold Arboretum, the late George B. Emerson, to write in his Trees and Shrubs of Mass., ed 2, 1: 161 (1875), under *Q. tinctoria:* "There are three pretty distinct varieties of the black oak. . . . These trees seem to be as different as the several varieties or species of the chestnut oak group. There are, probably, corresponding differences in the qualities of the wood." Nevertheless, so far as I have noted, most recent descriptions of what is taken as typical or average *Q. velutina* (or *tinctoria*) have studiously avoided the original diagnoses of Lamarck and of Michaux. Furthermore, we find characteristic drawings of leaves which strongly depart from the original illustrations cited by Lamarck or shown by Michaux, for recent drawings (such as those of Emerson, Faxon in Sargent's Silva and Manual, Hough, Dippel, Britton & Brown, Britton's North American Trees, Gray's Manual, the popular books of Mathews and others) all show a pinnatifid leaf with deep sinuses and elongate sharply toothed lobes. The characteristic leaves of the types of *Q. velutina* and *Q. tinctoria,* if mentioned at all, are usually treated as something quite atypical. Probably they are unusual on adult fruiting trees and to a great extent they seem to be juvenile or reversionary foliage, found on seedlings or saplings too young to fruit, and very generally on late sprouts coming out in August or September on the branches of trees from which the usual adult and pinnatifid leaves were stripped by caterpillars earlier in the summer.

To begin at the beginning, Lamarck's *Quercus velutina* was briefly but clearly described:

11. Chêne velouté, *Quercus velutina. Quercus foliis obovatis angulatis subtus brevissimè lanatis, angulis setá terminatis.* N. *An quercus humilis Virginiensis, castaneae folio.* Pluk. Alm. 309

[*i. e.* *Q. prinoides* Willd.].

β. Eadem foliis inciso-lobatis. N. ex Hort. D. Cels. Conf. *Quercus nigra.* du Roi. Harbk. p. 272. t. 6. f. I.

Ce *Chêne*, qui semble tenir le milieu par ses charactères entre l'espèce précédente [all-inclusive *Q. rubra* L.] & celle qui suit [*Q. nigra* L.], nous paroît ne devoir former qu'un arbrisseau. Il s'éloigne des *Chênes rouges* par ses feuilles ovales-obtuses, & veloutées ou comme drapées en dessous. Ces feuilles sont pétiolées & rétrécies en coin à leur base. Les pointes sétacées qui terminant leurs angles, ne permettent point de confondre ce *Chêne* avec l'espèce qui suit [i. e. *Q. nigra* L., including *Q. marilandica* Muench.].

Then, as an important item, Lamarck stated that he knew his *Quercus velutina* only imperfectly, having seen only a *very young* individual, said to have come from North America (Au reste, nous ne le connoissons qu'imperfaitement, ne l'ayant vu que fort jeune).

Lamarck's query as to whether his *Quercus velutina* might be what Plukenet had called "Quercus humilis Castaneae folio *Virginiensis* The Chinquapin Oake" at once suggests that the leaf of the type of *Q. velutina* could not have been the deeply pinnatifid one commonly illustrated under that name. Furthermore, his suggestion under *Q. velutina β*, "Conf. *Quercus nigra*. duRoi," not L., leads at once to DuRoi's figure (our PLATE I, *fig. 3*), which is certainly not deeply pinnatifid. Finally, the TYPE, preserved at Paris (our *figs. 1* and *2*), shows conclusively that Lamarck's species was indeed based on foliage of an "arbrisseau . . . fort jeune." This leaf is very closely matched by those of many specimens of saplings, such as shown on a "young tree in woods" from Fountain County, Indiana, *G. N. Jones* no. *15550*. Such a leaf is comparatively rare on fruiting branches but on sprouts coming out in August, on the branches of adult trees which have earlier been stripped, it is common. Incidentally, however, the leaf of the type of *Q. velutina* could almost as well have come from a sapling of Red Oak, *Q. rubra* L. (*Q. rubra maxima* Marsh. [1785]; *Q. ambigua* Michx. f. [1812], not Humb. & Bonpl. [1809]; *Q. borealis* Michx. f. [1817]; *Q. maxima* (Marsh.) Ashe [1916]). In fact, on reconsideration, Lamarck thought so himself, for after the publication by the younger Michaux of his *Q. ambigua* in 1812, Lamarck wrote on the original label of his *Q. velutina* "*Q. ambigua*. Mich."!

Leaving for a moment the question of *Q. rubra* L., we turn to *Q. tinctoria* Bartr. ex Michx. Hist. Chênes Am. no. 13 (1801), the name validated for the scarcely described *Q. tinctoria* of Bartram, Trav. 37 (1791), Bartram having simply "Gigantic Black Oak. Querc. tinctoria; the bark of this species of oak is found to afford a valuable yellow dye. The tree is known by the name of Black Oak in Pennsylvania, New-Jersey, New-York, and New-England." Whether a species is acceptably described merely by stating its colloquial name and its economic use without a single morphological character is very questionable. If that is all that is required the possibility of various upsets may well be considered. At any rate,

Michaux validated *Q. tinctoria* Bartram, and after Michaux's fuller description and illustration the name was almost universally used in the United States for the northern Black or Yellow-barked Oak or Quercitron, this general usage lasting for nearly a century—until the doubtful *Q. velutina* was picked up in 1892 by Sudworth and accepted by Sargent in his Silva in 1897.

Michaux's *Quercus tinctoria,* "foliis petiolatis, subtus pubescentibus, lato-obovalibus, leviter et subrotunde lobatis, basi obtusis," etc., consisted of two named varieties, each accompanied by a life-sized illustration of foliage and fruit, partly shown in our PLATE II, *figs. 1* and *4*. The foliage in both plates of Michaux is so similar that that of only one is here reproduced, but the cups were so distinct that they are reproduced as in the originals (*figs. 1* and *4*). The leaves, as will be seen, are not at all deeply lobed but are suggestive of the leaf of the type of the problematic *Q. velutina* Lam. The first of Michaux's two varieties, *Q. tinctoria angulosa,* the CHÊNE QUERCITRON *à feuilles anguleuses* (*fig. 1*), was assigned a synonymy including *"Q. Americana rubris venis,"* etc. of Plukenet, this being one of the basic synonyms, and possible source of the trivial name, cited by Linnaeus for his *Q. rubra* (1753); *Q. nigra* Marsh., not L., which had the leaves "irregularly and sometimes pretty deeply sinuated"; and *Q. velutina* Lam. In the first ("α") variety, *Q. tinctoria angulosa,* the cups were somewhat platter-like or saucer-shaped ("Cupula subscutellata . . . Cupule presque'en soucoupe") and their short scales appressed ("écailles peu adhérentes"), the cup and its scales (*fig. 1*) thus somewhat similar to those of *Q. ambigua* Michx. f. (1812), not Humb. & Bonpl., our *fig. 2,* or *Q. borealis* Michx. f. (1817), as well as of *Q. rubra* L., as shown by Sargent, Silva, 8: *t. ccccx, figs. 1* and *3* (our *fig. 3*)!

Under his second ("β") variety, *Quercus tinctoria* (*sinuosa*), shown in our PLATE II, *fig. 4,* Michaux cited the figure of *Q. nigra* sensu DuRoi, not L., our PLATE I, *fig. 3,* which Lamarck had earlier noted under his *Q. velutina. Quercus tinctoria sinuosa,* with "FOLIIS profundius sinuosis," although the profundity, as shown in his plate, was not very profound, otherwise differed from the first variety in its "Cupula turbinata" (our PLATE II, *fig. 4*), with the thin, lanceolate scales less tightly appressed, Redouté's (or Michaux's) figure well matching Faxon's in Sargent, l. c., *t. ccccxv, fig. 1,* of the fruits of *Q. velutina* (our PLATE II, *fig. 5*). The second half of *Q. tinctoria* was, then, referable to *Q. velutina* as interpreted by recent authors, the first half to *Q. rubra* L.

If it be urged that *Quercus velutina,* as described by Lamarck and as shown by the single leaf preserved, is not clearly definable exclusively as one species, and if it be admitted that Michaux's first variety of his *Q. tinctoria* was *Q. rubra* L., which is not generally used in dyeing, it might become necessary to face *Q. discolor* Ait. Hort. Kew. 3: 358(1789). In fact, *Q. discolor* antedated by two years Bartram's doubtfully acceptable description and by 12 years the validation by Michaux of his *Q. tinctoria,*

under which supposedly preferable name it rested as a synonym throughout that long period when neglect of strict priority was not a sin. Sargent, Trelease, and others regularly cited *Q. discolor* as a synonym of *Q. velutina* (or *tinctoria*), but Aiton's description was so discouragingly brief and inconclusive that it could have applied to any one of several species; and when Aiton stated that it was *Q. rubra* β. of Linnaeus he projected grave doubt into the situation, for, according to Sargent, Silva, l. c. 125, *Q. rubra* β. is not separable from *Q. rubra* (α), the species which some authors delight to call *Q. borealis* Michx. f. N. Am. Sylv. 1: 98, *t.26*(1817), the younger Michaux not wholly clarifying his very clear plate by retaining for it the earlier designation *Q. ambigua*! I do not know just what Aiton's type of *Q. discolor* was; if he were indeed correct in identifying it with *Q. rubra* β. of Linnaeus (1753), then those who would throw out the name *Q. rubra* L. as a *nomen confusum* should prayerfully consider the priority by 28 years of *Q. discolor* Ait. over *Q. borealis* Michx. f. Personally I am not now doing so, because of inadequate knowledge of what Aiton had. Nor am I throwing out *Q. rubra* L., the significance of that name having been sufficiently established by a century of good usage. As showing that the situation is not an absolutely simple one it is worth noting that *Q. discolor* had been introduced into cultivation in England as early as 1763 (Ait. l. c.). Lamarck's final comment after his description of *Q. velutina* twenty years later (in 1783) therefore becomes illuminating, but with a somewhat blinding light: "On le dit originaire de l'Amérique septentrionale: nous l'avons entendu nommer *Quercus desgulor anglorum*." Professor Arthur Stanley Pease informs me that, whereas "*Quercus*" and "*anglorum*" are perfectly evident, "*desgulor*" is not Latin. "Could that by any chance be a mistake, due to someone's faulty hearing of *discolor?* Is there any oak which the English botanists had called *Q. discolor?*" In view of the fact that the Lamarck specimen was a sapling raised at Paris, it is not at all improbable that it was derived from the tree cultivated in England and later published as *Q. discolor* Ait. I do not know on what evidence *Q. discolor* was placed by Sargent and by Trelease in the synonymy of *Q. velutina.*

Coming down to Earth, we have the situation which recurs in case of very many of the earlier American species described in Europe, without any clear understanding of our plants. When Linnaeus, Aiton, or Lamarck based a species on a single cited specimen all was well; when they cited two, confusion was probable; when they based species on several citations and quite uncoördinated specimens, confusion became confounded. Nevertheless, if we should start in to reject all the Linnean names of this sort as *nomina confusa* the wreckage would be enormous. What real good would be accomplished, except the satisfaction of a mechanical theory? No theory (not even attempts to "standardize" colloquial usage) ever established a language or its use. The well known and common *Asplenium platyneuron* (L.)Oakes would be rejected, for the basic *Acrostichum*

platyneuron L. would have to go because Linnaeus included under his binomial not only an *Asplenium* but members of *Polypodium*. *Scirpus capillaris* L. (nomenclatural basis of *Fimbristylis capillaris* (L.) Gray, *Stenophyllus capillaris* (L.) Britton, and of *Bulbostylis capillaris* (L.) C. B. Clarke — *Bulbostylis* a conserved name), "*Habitat* in Virginia, Aethiopia, Zeylona," was a mixture of several species and at least two genera; yet the trivial name has been fixed by usage ("established custom") ever since it was restricted by Roemer & Schultes in 1817, and no good would result from now suddenly declaring it a *nomen confusum*. Surely *Quercus velutina*, as described by Lamarck and as shown by his preserved specimen, is pretty vague. *Quercus tinctoria* of Michaux consisted of two specific elements, the first not belonging to *Q. tinctoria* as interpreted for a century.

Or take a very simple case, that of *Fraxinus americana* L. Sp. Pl. 1057(1753):

3. FRAXINUS foliolis integerrimis, petiolis teretibus. *Gron. virg.* 122. *Roy. lugdb.* 533.
Fraxinus caroliniensis, foliis angustioribus utrinque acuminatis pendulis. *Catesb. car.* I.*p*.80.*t*.80.
Habitat in Carolina, Virginia.♄

That is a relatively uncomplicated account but it has its entanglements. The Catesby plate (a portion shown in our PLATE III, *fig. 1*) of his *Fraxinus caroliniensis*, etc. of "low moist places" in Carolina, shows a characteristic fruiting branch with the small oblong leaflets acuminate at both ends, and the very distinct fruit of the southern Water- or Swamp-Ash, the characteristic small tree of southeastern swamps and very abundant in both Carolinas and eastern Virginia, "with," to quote Sargent's Silva, "elongated stout terete pale petioles"; whereas the White Ash, the *Fraxinus americana* of all recent authors, has, as Sargent correctly says, "stout grooved petioles," etc. Gronovius gave nothing not covered later by Linnaeus, and he, likewise, cited Catesby's description and plate. Royen simply abbreviated the Gronovian account but included the Catesby reference. In view of the "petiolis teretibus" of the Linnean diagnosis, the citation by him of a single plate, and his citation first of Carolina, a perfectly rational case could be made out for using the name *Fraxinus americana* L. (1753) for the southern Water-Ash which we all call *F. caroliniana* Mill. (1768). We should then be forced to call the common northern White Ash either *F. nova-anglia* Mill. (1768), *F. acuminata* Lam. (1786), or *F. caroliniensis* Wangenheim (1787), according to which of these, on careful comparison of the types, proved to have right of way; it would be ironical if Wangenheim's name won the competition!

My point is just this: the evidence of the Linnean account and the one plate which he cited lead directly to *Fraxinus americana* as the name for the southern Water-Ash; but one final point, often neglected by those who invoke the principle of *nomina confusa*, saves the day. Linnaeus had in his herbarium, when he prepared the *Species Plantarum* of 1753, a speci-

men which he marked as no. "3. *americana*" (our PLATE III, *fig. 2*). Only by taking as the TYPE this badly defoliolated specimen, showing dentate round-based leaflets (a characteristic leaf of a species with "grooved petioles") can we save the name *F. americana* in its familiar sense. Yet this is exactly what we have to do in a great number of cases, or else abandon some of the most familiar names or, most unfortunately, reverse their significance.

When the unquestioned type has been hopelessly misinterpreted and there is no way out we must make the change, but when a Linnean species was a confusion of several elements, as in *Quercus Prinus* and *Q. rubra*, the case approaches that of *Fraxinus americana*, just discussed. Sargent, Silva, 8: 53, using the name *Quercus Prinus* L. in its long-restricted sense of *Q. Prinus* (*monticola*) Michx. or *Q. montana* Willd., said in a footnote (footnotes have a way of being given the principal weight!): "The early description of the Chestnut Oak might apply as well to the Swamp Chestnut Oak (*Quercus Michauxii*) as to this species, which does not grow near the coast of Virginia, where, however, the Swamp Chestnut Oak is common." That was the entering wedge; forthwith the name *Q. Prinus* was transferred by the credulous to the latter. However, as Svenson pointedly says in Rhodora, 47: 365(1945), "To this may be replied that Banister, who collected much of the early material described by Plukenet, did not lose his life by falling off a mountain on the coastal plain," Banister living "on the coast" of Virginia, only about 10 miles from Clayton's home. Furthermore, the Rock Chestnut Oak (*Q. montana*) occurs in the right situations (dry rocky slopes) not only near Clayton's home but in a number of counties to the south and southwest, where, if there are any disbelievers, I shall be glad (if they pay the bills) to show it within sight of transatlantic freighters steaming up the lower James! Since, as Svenson shows, Linnaeus himself marked specimens of this oak as *Q. Prinus*, what but confusion results in a change in the application of the name, especially when the new interpretation is based upon wholly erroneous and theoretical assumption?

Similarly with *Quercus rubra* L. That name covered many (if not most) of the eastern species of subgenus *Erythrobalanus* as now understood, but the northern Red Oak was just as much among them as any of the others. In 1916, however, Sargent in Rhodora, 18: 46, suddenly reversed the long-established usage by stating his opinion that "the name *Quercus rubra* Linnaeus must be transferred to the tree which later was called *Quercus falcata* by Michaux, the Red Oak of the southern states." If typification is to rest primarily on colloquial names it is important to check the facts.

In his original publication of *Quercus falcata* Michx. Hist. Chênes Am. no. 16(1801), the elder Michaux called it "DOWNY RED OAK." Michaux filius, who knew vastly more than any predecessor (or most successors) from first-hand experience with eastern North American trees, called it in his Hist. Arb. Forest. Am. Sept. 2: 104(1812) only "SPANISH OAK," and he then explained, as he did again, in English, in his No. Am. Sylva, 1: 87

(1817), under "SPANISH OAK," that "In Delaware, Maryland and Virginia, it is known only by the name of Spanish Oak, and in the Carolinas and Georgia by that or Red Oak." Now checking on the names used in the period following Michaux but before the colloquial names were factory-made, we get interesting results. Stephen Elliott, Sketch Bot. S. C. and Ga. 2: 605(1824), under the very strikingly different *Q. falcata* var. *triloba* (Michx.)Nutt., said of colloquial usage in South Carolina and Georgia: "These two trees are called by the inhabitants Red Oak or Spanish Oak. Where I have seen any distinction made, Red Oak was applied to the Q. Triloba — Spanish Oak to the Q. falcata." Croom, Cat. Pl. New Bern, N. C. 30(1837) has *Q. falcata* simply as *"Black oak,"* thus entering a new competitor! Darby, Man. Bot. So. States, 316(1841), gave for *Q. falcata* only "Spanish Oak." M. A. Curtis, Geol. Nat. Hist. Surv. N. C. pt. III.35 (1860), enumerating the oaks of the state, had "Spanish Oak (Q. falcata.)" and "Red Oak (Q. rubra.)," but on p. 39, under "SPANISH OAK. (Q. falcata, Michx.)" he said: "This is generally known in this state, I think, by the name of *Red Oak,* though sometimes called as above. It is also, in some parts, denominated *Turkey Oak,* from a vague resemblance between the form of the leaf (when it has but three divisions) and the track of a Turkey." Porcher, writing of the practical uses of plants among the people of South Carolina, in his Resources of So. Fields and Forests, 256(1863), called *Q. falcata* "Spanish Oak," Porcher stating that "In domestic practice, where an easily obtained and efficient astringent is required, this, and the more common species, the *Q. rubra* [in the long-established sense], are of no little value. They are used to a large extent on the plantations in South Carolina." If anyone knew about such uses in South Carolina, certainly Porcher did. His statement gives support to the much earlier one of Brickell in 1737, Nat. Hist. N. C. [repr. without date, by the Trustees of Public Libraries of N. C.], 60, Brickell saying: "The *Spanish Oak* has a whitish smooth Bark [Sargent, Silva, 8: 147, says "sometimes pale"] . . .; the Bark of this Tree is used for the Cure of the *Yaws*." Not quite so early was John Clayton's "Quercus rubra seu Hispanica hic dicta, foliis amplis varie profundeque incisis," in Gronovius, Fl. Virg. ed. 2, 149(1762), for when, in 1839, Asa Gray examined these Clayton plants, he wrote against this no. (785) in his copy of Gronovius *"Q. falcata."* It is not necessary to draw in Clayton's further comment, "Cortex ad corium depsendum utilissimus" and to argue that he referred to the "Cure of the *Yaws*." "Could be!" The early use of the name "Spanish Oak" for typical *Quercus falcata* must be apparent, although from Virginia southward the name Red Oak was also sometimes used.

Sudworth, in his Nomencl. Arb. Fl. U. S. 171(1896), enumerating the states where the colloquial names are used, but using the name *Q. digitata* for *Q. falcata, Q. triloba* and *falcata,* var. *pagodaefolia* Ell., gave "Spanish Oak" preference, this name for *Q. falcata* (*digitata*) being used in 12 states, including "South Carolina, North Carolina, Virginia, Delaware and

Pennsylvania"; while "Red Oak" had been found in use for this species in 8 states, the northeasternmost being North Carolina and Virginia. Later, however, in his Check List For. Trees U. S. (1927), Sudworth, following Sargent's lead, wrote of the "tree we have been calling Spanish Oak" which "must, therefore, be called *Quercus rubra* Linnaeus. Notwithstanding the fact that this oak has long been known . . . as Spanish Oak. . . It seems advisable, therefore, to discard the name 'Spanish Oak' and to take up Southern Red Oak," just as if this edict from Washington would change the actual usage of such unschooled woodsmen as have always called it "Spanish Oak," "Turkey-Oak" or even "Black Oak." In this volume, however, Sudworth gives a reenumeration of states in which the various colloquial names are used: "Spanish Oak" in 12, including "Del., Md., Va., N. C., S. C.," etc.; "Red Oak" in 10, the northeasternmost being "N. C., Va."; "Southern Red Oak" in none. Therefore, by his strange method of counting the ballots, the "NAME IN USE" is "Southern Red Oak." *Standardized Plant Names* has no monopoly in deciding what names are in actual use among "the people."

My point in all this is as follows: since the sum-total of evidence from those who early wrote of southern trees from first-hand knowledge of them is that the name "Spanish Oak" was, before modern dictatorial days, more generally used for *Q. falcata* than the name "Red Oak" (used more generally in the South for the traditional *Quercus rubra*), the argument that by *Q. rubra* of "Virginia, Carolina" Linnaeus really meant *Q. falcata* seems to me a forced one. Sudworth, in 1897, had enumerated 27 states (all in which it occurs) where "Red Oak" was used for *Q. rubra* of practically all botanists down to Sargent in 1916. Since the name of this species suddenly and quite unjustifiably has been changed to *Q. borealis* its "NAME IN USE" suddenly changes to "Canadian Red Oak" or "Northern Red Oak." *C'est à rire!*

Nothing but confusion arises from shifting the name *Quercus rubra* to the very different southern *Q. falcata,* which has honorably borne that name for nearly a century-and-a-half, especially since *Q. rubra* in its traditional sense was among the specimens so marked by Linnaeus. If the argument is pressed that *Q. rubra* L. was a *"nomen confusum,"* we shall have to face the same argument regarding hundreds of other names which had a tangled beginning. It seems to me that in these cases, as in those of *Quercus velutina* and *Fraxinus americana,* the cause of real understanding and progress is best served by following the *spirit* more definitely than some imagined *"letter"* of the International Rules; and in holding such names as were based demonstrably in part on the plant long accepted as typical. Naturally, there are left many names which have from the first been misapplied. In these cases change is unavoidable. When, however, long-established and universally understood names can legitimately be preserved, why seek reasons to change them? One of the Guiding Principles of our International Rules (Art. 5) reads: " . . . where the con-

sequences of rules are doubtful, established custom must be followed." The earlier wording was better: "established custom becomes law."

EXPLANATION OF PLATES

PLATE I

FIGS. 1 and 2. The TYPE and labels of *Quercus velutina* Lam. (after *Cintract*), FIG. 2 showing Lamarck's reference to DuRoi's illustration of *Q. nigra* sensu DuRoi, not L., with which Lamarck thought *Q. velutina* might be identical, and his later identification of *Q. velutina* with *Q. ambigua* Michx. f. FIG. 3. DuRoi's illustration of his *Q. nigra*.

PLATE II

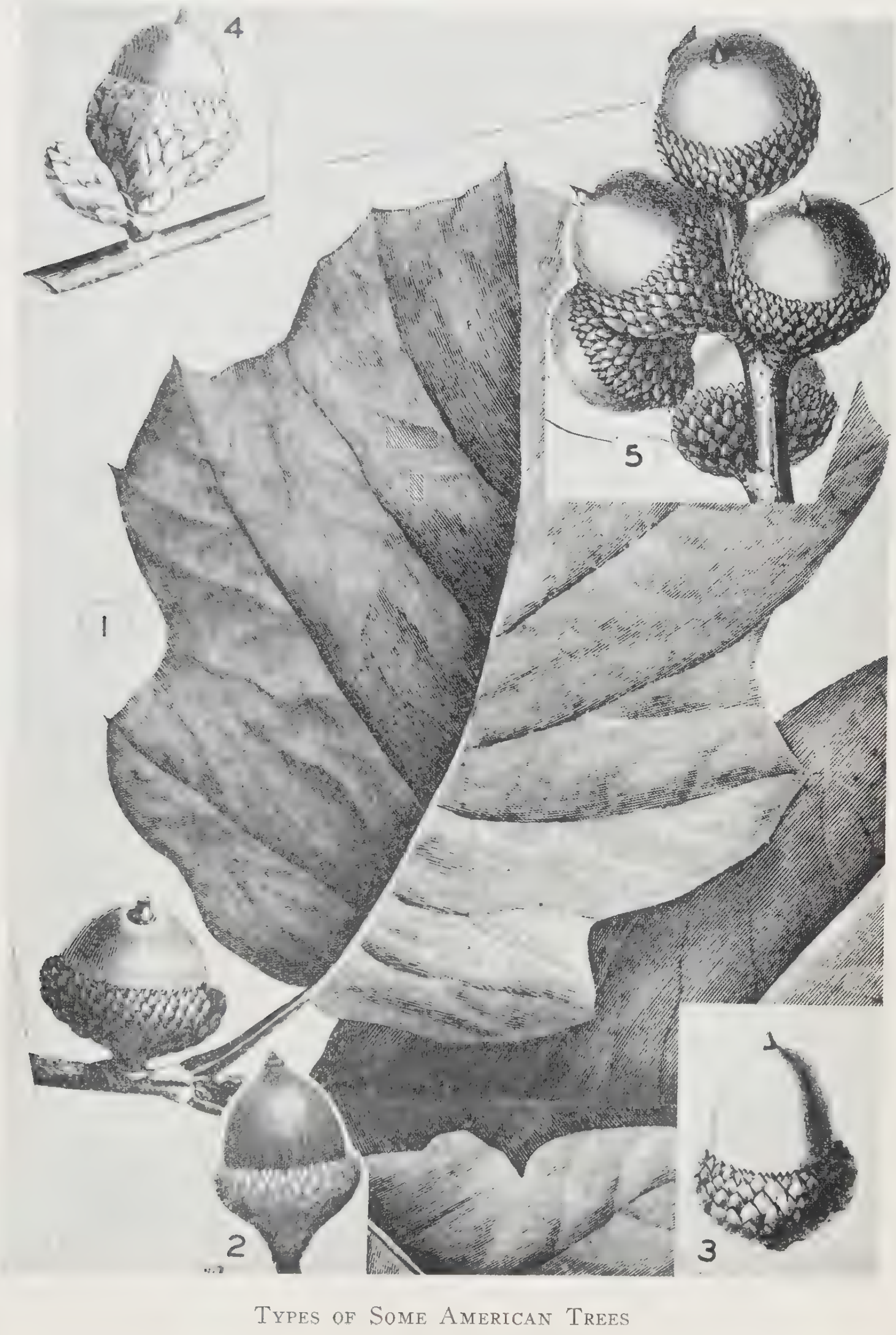
FIG. 1. Portion of the original illustration of *Quercus tinctoria angulosa* Michx. FIG. 2. Fruit of *Q. borealis* Michx. f., 1817 (*Q. ambigua* Michx. f., 1812, not Humb. & Bonpl. [1809]), from the original plate. FIG. 3. Fruit of *Q. rubra* L., after *Faxon* in Sargent's Silva. FIG. 4. Fruit of *Q. tinctoria* (*sinuosa*) Michx. from the original plate. FIG. 5. Fruits of *Q. velutina,* after *Faxon* in Sargent's Silva.

PLATE III

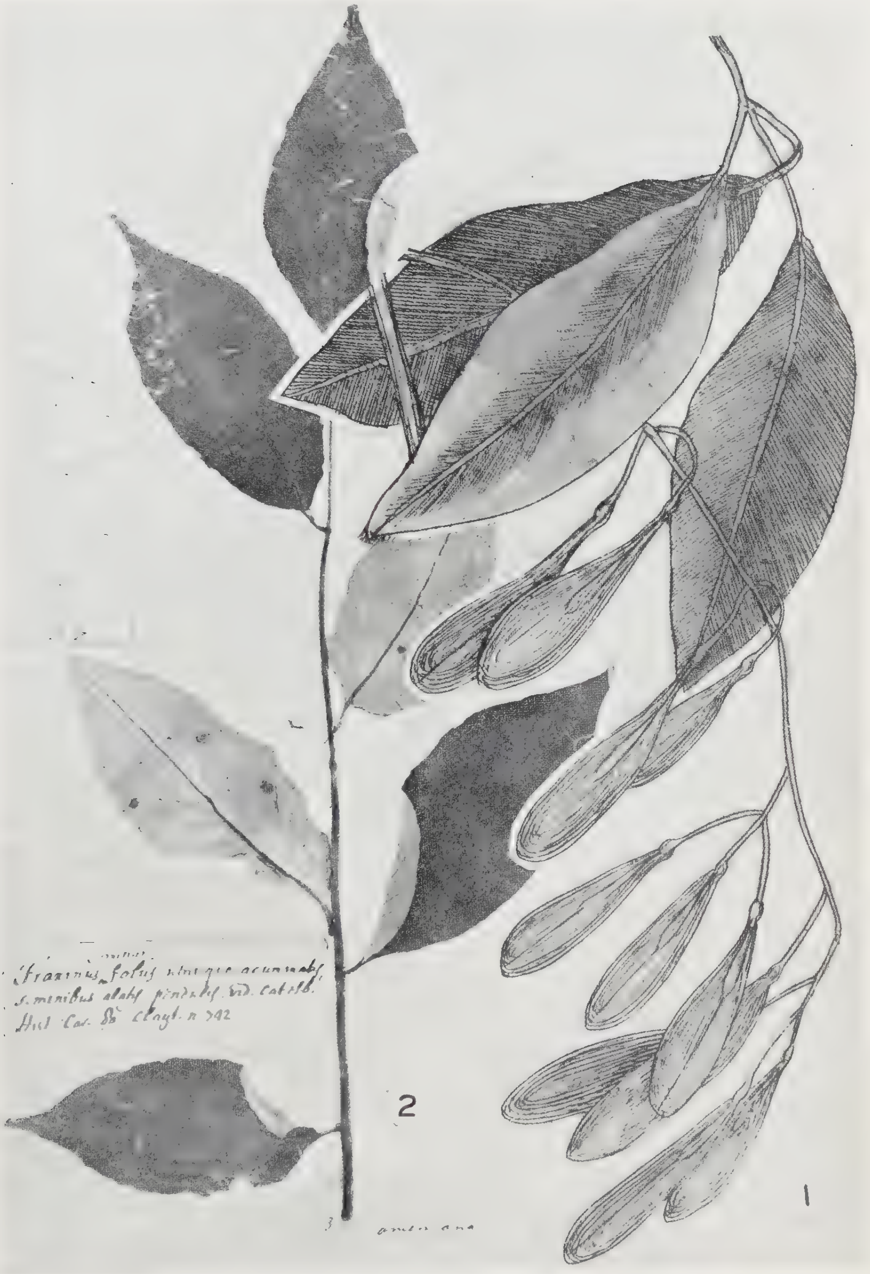
FIG. 1. *Fraxinus caroliniensis, foliis angustioribus utrinque acuminatis pendulis* of Catesby, the illustration cited by Linnaeus as his *Fraxinus americana.* FIG. 2. The specimen (courtesy of Mr. *S. Savage*) marked by Linnaeus "3 americana" in his own herbarium prior to 1753, this specimen accepted as the TYPE of the species.

GRAY HERBARIUM,
HARVARD UNIVERSITY.

Types of Some American Trees



Types of Some American Trees



Types of Some American Trees

FOOD PLANTS OF THE INDIANS OF THE GUATEMALAN HIGHLANDS

Paul C. Standley

Four hundred and twenty-five years ago Pedro de Alvarado led a little band of Spanish soldiers and a host of Mexican mercenaries out of Mexico across the Río Suchiate into Guatemala. When they reached the highlands of Quezaltenango, they entered a densely inhabited region that extended all the way across the mountains (Los Altos) as far as the present site of Guatemala City. The density of the population is attested by contemporary writers like Bernal Díaz de Castillo, by extensive ruins of such magnificently located cities as Utatlán and Zaculeu, and by reports of other towns of which no visible trace remains.

Just outside Xelajuj, now Quezaltenango, the Spaniards fought a great battle that resulted in slaughter of myriads of Indian warriors. The Río Samalá, a tranquil mountain stream, is said to have run red with blood, causing the horror-struck Indian survivors to name it the "River of Blood," a name it still bears. In that battle and in ensuing ones, perished the flower of Indian aristocracy. Thus today there are few descendants of the upper classes, who according to all testimony were a group much superior to the rude hunters and tillers of the fields.

The highland plains and valleys were densely populated in preconquest times and may well have had more inhabitants than now. Their people, although less advanced than those of the Valley of Mexico and Yucatán, had achieved a relatively high degree of culture. There is ground for belief that they lived under conditions little if at all inferior to those of rural Iberians of 1500 or perhaps even of 1946.

The Guatemalan Indians are among the most conservative peoples of the earth. After four centuries of exposure to Iberian culture they have changed their customs but little. Their clothing is different because of the introduction of sheep and imitation of early Spanish costumes. They have adjusted their pagan rites comfortably to the forms of Christian religion. Many of their dwellings scarcely are of aboriginal type but are copied from those of the Spaniards. They now have pigs and lard to improve their former food, although any meat they get from these or other imported animals is no important element of their diet. Otherwise the highland Indians subsist much as did their remote ancestors.

Their diet is probably no better and no worse. They eat little meat now since they have few domestic animals except sheep, whose chief product is not meat but wool. In preconquest days their only edible domestic animals were turkeys and perhaps a few ducks, and except in homes of the upper classes meat must have been a rarity. Wild animals

large enough for food are scarce in Guatemala now, and probably they never were much more plentiful after the land had been settled.

Guatemala has climates suitable for growth of any plant of the earth. Many exotic ones have been introduced since the Conquest, and in the markets of the larger cities are displayed most of the important fruits and vegetables of all tropical and temperate climes. The only vegetable I never have found there is the parsnip. There have been introduced other vegetable crops such as coffee and sugar, but these, produced in vast quantities in Guatemala, are little known to the highland Indians and used less.

Coffee and sugar are not grown in the highlands, and the Indians know them only as luxuries. As for Old World vegetables, I suspect the Indians simply do not care for them. They do cultivate them for the *ladino* markets of Guatemala and Quezaltenango, and make a good living by doing so. It would be hard to discover finer vegetables than those of the irrigated valleys of Almolonga and Zunil, near Quezaltenango, but those Indians are rather sophisticated, and long ago devised the best methods of cultivating them for the *ladino* trade.

Despite very liberal and successful introduction of fruits, vegetables, and cereals into Guatemala from abroad, highland people subsist upon the same vegetables and cereals, cooked in the same ways, as they did 500 years ago. The single important exception is the potato, brought probably soon after the Conquest from Peru or Chile, and now planted throughout Los Altos. It is grown at higher elevations than any other crop, unless it be maize.

What were the food plants of the early Guatemalans? There were only two really important ones, maize and beans, or *frijoles*. Maize in the form of tortillas and *frijoles* constitute practically the whole diet of the highland Indians, and anything else they may eat is mere lagnappe. This was the diet of their ancestors. The antiquity of maize and beans in Guatemala can be deduced from the great variation that both exhibit. Their varieties often are very local and carefully guarded, but not because they are believed superior to varieties grown by neighbors. The Indians cherish a firm belief that it is best to plant seeds grown on the premises. Otherwise the plants never would be happy; they would become homesick, as it were, pine away, and the crop would fail.

It is fortunate that maize and beans together form a moderately nutritious and balanced diet, for it is practically all that the Indians, or the *ladinos* for that matter, have to eat. One used to the fare of North America or continental Europe will find this diet heavy, difficult of digestion, and flavorless. Even the Indians find it so, and long ago they learned to flavor it with the native chile (*Capsicum*). Guatemalans, unlike Mexicans, seldom use chile to excess, but they use it enough and sometimes fortify it with a little imported garlic.

Another ancient vegetable used primarily for flavoring is the tomato, which may have been brought by the Spaniards from Peru. It does not

behave here as a native plant, never is found truly wild, and is attacked by many pests. It is said that if a Guatemalan cook goes into a kitchen and does not find tomatoes there, she walks out, refusing to start a meal. The highland Indians are less temperamental. An excellent substitute for tomato is the ground-cherry (*Physalis*), used not like a fruit as in the United States, but in cooking exactly like the tomato. Great quantities of *tomatillos* are traded in the markets, some of them as much as two inches in diameter and looking like small, green or yellow tomatoes.

An aboriginal vegetable of Central America is the pumpkin. It has no close wild relative in North America, although there are native wild species of *Cucurbita* that are inedible. It should be emphasized that the "foods" of the Guatemalan Indians were originally and still are maize and beans. Other edible plants, of scant nutriment, are merely *verduras* or "greens," which serve principally like the roughage fed to cattle, or as appetizers. Fruits, likewise, are not considered real food but are eaten because they taste good. The poorer people of Guatemala, and especially the Indians, seldom place fruits on the table but merely eat or "suck" them between meals.

As for pumpkins, most Guatemalan varieties have little resemblance to common pumpkins of the United States. Their long cultivation has established many well-marked forms, almost unlimited in number as one sees them in the markets, yet certain common varieties of other Central American countries, like the little *pipián* of Salvador, which is eaten only when very immature, are lacking in Guatemala.

Tomatoes and pumpkins were by no means the only secondary vegetables grown by the ancient Guatemalans, nor the only ones cultivated today by the Indians. An important one, known only in cultivation, is the chayote, the *güisquil* or *huisquil* of Guatemala. Although the chayote is grown throughout southern Mexico and Central America, there seem to be many more varieties in Guatemala than elsewhere. They are large or small, green or white, spiny or unarmed. In the Department of Huehuetenango there are fantastic forms, large fruits so densely armed with long, flexible but still rather stiff spines that it is unpleasant to handle them. The chayote plant is almost unique because every part can be eaten except when old and tough. The fruits are an excellent vegetable that can be cooked in many ways. The tender immature seed or *lengua* is a delicacy pressed upon guests; the young shoots, inflorescences, and fresh leaves are a common *verdura*. The huge roots, which may be removed without killing the plant, are a good vegetable, and also are the basis of a tasty dessert that has a strange consistency almost like wood shavings.

One vegetable that is Guatemalan *par excellence* is the pacaya, the staminate inflorescence of a low slender palm of the genus *Chamaedorea*. Pacayas are not confined to Guatemala, as some ill-informed or disingenuous persons would have us believe, nor are they the product of a single species of *Chamaedorea*, even within Guatemala. Those of Guatemala are so much more abundant than those of other countries and so much better in

quality that Guatemala has some justification for claiming a monopoly of them. The finest are those grown about Cobán in Alta Verapaz, most of which are cultivated in regular plantations, and transported by truck-load to Guatemala and other cities. Their cultivation upon a small scale is probably ancient, the palms having been planted about dwellings because their natural home was in distant mountain forests, where it was not always easy to get them when wanted.

The pacaya is one of the most delicious of Central American vegetables. The plants are dioecious, and only the staminate spadices are eaten. With their enveloping spathes, these resemble roasting ears with their husks and sometimes are quite as large. When "husked" or opened, there is exposed an intricate mass that suggests a cluster of white worms. This part of the pacaya is dipped in egg and fried, or cooked in other ways. It may be boiled and seasoned with oil and vinegar, and eaten raw it makes a savory salad. Pacayas always have a slightly bitter flavor that is agreeable, and no matter how prepared for eating, they always are good.

Another vegetable that is planted, or at least never grows really wild, is the local Yucca or *izote*, *Yucca elephantipes*. This may have been brought to Guatemala from Mexico by the mercenaries hired by the Spanish conquerors, but it may have reached Central America earlier on the backs of the traders that wandered, as they do today, hundreds of miles north and south trading in products of different regions of Mexico and Central America. Yucca flowers are so liked that it is unusual to find one of the treelike plants with a full-blown inflorescence. While still in bud, the flowers are gathered, cooked, and eaten. They afford a good vegetable when dipped in egg and fried, and probably they would make a good salad. They are abundant and substantial enough to make a filling food.

The *chaya*, *Cnidoscolus aconitifolius*, is rather scarce in Guatemala and may be a recent introduction from Yucatán. It is a large shrub or small bushy-topped tree with an abundance of deep green, rather succulent foliage that is cooked and eaten. Introduced experimentally into southern Florida, it has been found that the leaves are particularly rich in certain vitamins; thus the *chaya* may enjoy a brief popularity among food faddists.

The Guatemalan vegetables brought under cultivation by the Indians presumably were those of greatest food value and easiest adaptation to cultivation, or ones that could not always be found wild when wanted. The aboriginal people, like their descendants, used as food a substantial number of plants that were edible, more or less agreeable in taste, but grew so generally about settlements that cultivation was unnecessary. These plants never have been "improved" like beans, pumpkins, and tomatoes, and they seem to vary little, no matter how varied their natural habitats. These esculent plants are rather numerous, but only a few can be noted here.

Purslane or pusley (*Portulaca oleracea*) sometimes is eaten as a pot herb in the United States, but in Guatemala its use is common and doubtless of great antiquity. Its good quality and abundance make it unneces-

sary to plant spinach in Central America. Another plant of the same family, *Calandrinia micrantha*, often is eaten like spinach. Much more popular are several native species of *Crotalaria*, known locally as *chipilín* (an Aztec name), whose young shoots, leaves, and flowers are cooked and eaten. They, like many edible wild plants, are sold in huge amounts in the Indian and *ladino* markets.

A favorite pot herb of the Guatemalan Indians is our common black nightshade, *Solanum nigrum*. Large quantities of the tender foliage with the flowers and young fruits are gathered and either consumed at home or sold in nearby markets. This plant, known in Guatemala as *yerba mora* or *mucuy*, is cooked like spinach, or used to fill tartlike *empanadas*, small turnovers filled with every conceivable mixture of greens, vegetables, meats, raisins, fruits, and other articles that it is best not to investigate too closely.

Blossoms of red-flowered Erythrinas are cooked like string beans and eaten, and made into a sort of fritter. The immature and still tender seed pods of *Gonolobus* are cooked and eaten as a vegetable. One of the favorite "greens" of Guatemala is the young shoots and flowers of *Fernaldia*, a genus of Apocynaceae, known in Guatemala and Salvador as *loroco*. Young sprouts of the Bromelias are much used as food, especially in arid parts of eastern Guatemala. One scarcely would expect that their usually stiff and spine-edged leaves could be eaten, but of course only the tenderest ones are gathered. It is hard to believe that even those can be a delectable vegetable. I have not had an opportunity to sample them.

A most unusual vegetable, fairly common, consists of the tender young flower heads of the Calatheas, which are dipped in egg or batter and fried or broiled. Equally strange are the young inflorescences of the aroid genus *Spathiphyllum*, which are treated in the same manner. The spadices in this genus look much like embryonic ears of corn. Some years ago, it is related, a North American, possibly a tourist, reported to the U. S. Department of Agriculture that in Guatemala he had been served soup of which miniature ears of corn were an ingredient. One may imagine the thrill with which this news was received, and the disgust of the men sent by the Department to investigate the matter. The credulity of scientists knows no bounds, and marvels still are expected from other continents besides Africa.

This year the world has heard a great deal about famine. In Guatemala famine is nothing new. When the maize crop fails, the result is catastrophic in a region where the diet at best is scant. In recent years the government has found temporary means of alleviating such disasters, but only a few years ago the highland Indians often suffered severely, and the results were quite as bad when clouds of locusts invaded the corn fields of the Pacific lowlands. In such cases the people had to resort to any vegetable matter that would sustain life. One of the plants used at such times was one or more wild species of *Dioscorea*, called *madre de maíz*, whose large hard roots were made into a kind of tortilla or tamal. Even

more use was made of the large seeds of *Brosimum*, which were boiled, ground, and made into coarse tortillas. Only a few years ago a scientist of the U. S. Department of Agriculture soberly suggested in print the planting of a large part of the Florida Peninsula with forests of *Brosimum Alicastrum*. Whether the trees would grow there is dubious, but if they did, one suspects that the good people of Florida, for whose welfare so much solicitude was expressed, would care less for cakes of *Brosimum* seeds than for fried chicken, ice cream, or even grits. It is only when starving that Guatemalan Indians condescend to eat them.

The leaves of *Eryngium foetidum* and *Chenopodium ambrosioides*, both plants of incomparably vile odor, give a pleasing or even delicious flavor to soups and meat stews. It must have been in time of famine that the Indians discovered the comestible value of plants so unpromising.

These are only a few random notes on edible plants of Guatemala, presented in no orderly fashion. One plant not yet mentioned, but one for which Guatemala is famous, is the avocado. No region of the earth produces better avocados; few regions ones of comparable quality. Their food value is high because of the large amount of oil in the flesh, and the mountain Indians enjoy eating their hard-skinned avocados for both their food value and their delicious flavor.

Although from a botanical standpoint indubitably a fruit, the avocado is regarded by Guatemalans as something else, as is the tomato in the United States. At a hotel table in the town of Jutiapa one day, some regular patrons who formed a sort of lunch club demanded the usual "fruit" that should accompany the noonday meal. The French housekeeper explained tactfully that fruit was scarce in the market now, in the middle of the dry season; however she *could* give them some avocados. Uproarious shouts greeted this hopeful offer. For the rest of the meal every new guest to enter the dining room was greeted with the story, which ended: "Figúrese! We asked Madame for fruit, and she offered us *avocados*!"

CHICAGO NATURAL HISTORY MUSEUM.

A CRITICAL STUDY OF PHILIPPINE SPECIES OF THE TRIBE AQUILARIEAE, FAMILY THYMELAEACEAE*

EDUARDO QUISUMBING

THE TRIBE AQUILARIEAE (R. Br.) Baill. (1877); Gilg (1894) is represented by five genera: *Aquilaria* Lam., *Gyrinopsis* Decne., *Brachythalamus* Gilg, *Gyrinops* Gaertn., and *Lachnolepis* Miq. These genera have been much confused and no two authors can agree on their status. Even the well known genus *Aquilaria* is badly defined and the species, in general, are inadequately known. Hallier[1] reduced the four small genera *Gyrinops*, *Gyrinopsis*, *Brachythalamus*, and *Lachnolepis* to *Aquilaria*. Hallier grouped the species of *Aquilaria* under six sections: *Agallochum*, *Gyrinopsis*, *Amphinoma*, *Brachythalamus*, *Gyrinops*, and *Lachnolepis*. His third section seems ill-founded. *Aquilaria khasiana* Hallier, the only species under this section, appears to be but a mere form of the more familiar *A. Agallochoa* Roxb. On the other hand, on account of the presence of five stamens, I agree with Domke[2] that *Brachythalamus* is similar to *Gyrinops*. The shape of the perianth-tube is more like that of *Gyrinopsis*, which is slender and tubular. The presence of five stamens places *Lachnolepis* under *Gyrinops*. As to *Gyrinopsis* I concur with Merrill[3] that it is distinct from *Aquilaria*. In addition, I feel that the form of perianth-tube is a major distinguishing feature between the two genera, as well as the relative position of the nectarial scales, and the filaments. The development of the fruit is a distinguishing character in *Aquilaria* (*A. sinensis* and *A. malaccensis*), the fruit developing at the summit of the receptacle over the perianth. In *Gyrinopsis* (*G. Cumingana* et al.), the fruit develops and breaks at the side of the perianth-tube. As to *Gyrinops*, typified by *Gyrinops Walla*, I am convinced that it is distinct from the two genera. *Aquilaria* and *Gyrinopsis* are characterized by having ten stamens; *Gyrinops* has five or six stamens, normally five. Hallier discounts the value of the number of stamens as a distinguishing feature of the genera *Aquilaria* and *Gyrinops*. In this connection Hallier[4] expresses his views thus:

* The study upon which this treatment is based was essentially completed before the recent war, during which the herbarium and library of the Bureau of Science, Manila, were destroyed. Of the two new species of *Gyrinopsis* here proposed, isotypes were sent to the herbaria at Singapore and Buitenzorg and are also to be found in some American and European herbaria.

[1] H. Hallier in Med. Rijks Herb. Leiden, 44: 1–31. 1922.

[2] Domke in Notizbl. Bot. Gart. Berlin, 11: 349. 1932.

[3] Merrill in Philip. Jour. Sci. Bot. 7: 313. 1912.

[4] H. Hallier in Med. Rijks Herb. Leiden, 44: 5. 1922.

"So hätten wir denn nur noch zwei Gattungen, nämlich *Aquilaria* (mit Einschluss von *Gyrinopsis*) und *Gyrinops* (mit Einschluss von *Lachnolepis* und *Brachythalamus*), die widerum durch die einander sehr ähnlichen Kapseln der *A. khasiana* m. und der *Gyrinops Walla* auf's engste mit einander verknüpft werden, sich im übrigen aber nur durch das Vorhandensein oder Fehlen der fünf Kronstaubblätter von einander unterschieden. Auch auf letzteres Verhältnis darf jedoch nicht allzuviel Gewicht gelegt werden, da auch bei den vermütlichen Stammeltern der Thymelaeaseen, sowie der ganzen Myrtinen, der Polygalinen. . ."

Apparently the genus *Gyrinopsis* was not known to Hooker.[5] He recognized but two genera (*Gyrinops* and *Aquilaria*) under the tribe AQUILARIEAE. Of note is the way he differentiates the two genera, on the basis of the form of the perianth and the number of stamens.

While in some genera the number of stamens varies, in others this feature is important and of a major character. I consider, in this particular case, this feature a distinguishing one.

This paper includes descriptions of two apparently new species of *Gyrinopsis* (*G. parvifolia* and *G. pubifolia*). Because of a critical study of the group a few nomenclatural changes are in order.

In conclusion, it seems best to recognize three genera (*Aquilaria, Gyrinopsis,* and *Gyrinops*) in this group of allied plants. They may be separated on technical characters as follows:

1. Stamens 10.
    2. Perianth-tube campanulate or infundibuliform; stamens stalked; fruit developing on the summit of the perianth; seeds with umbilical cord. ....1. *Aquilaria.*
    2. Perianth slender, cylindric; stamens sessile; fruit developing from the side of the perianth-tube; seeds without umbilical cord. ....2. *Gyrinopsis.*
1. Stamens 5; perianth cylindric. ....3. *Gyrinops.*

Aquilaria Lamarck

Aquilaria Lam. Encycl. **1**: 49. 1783, **2**: 610. 1788, Illus. **2**: *t. 356.* 1799; Cav. Diss. 377, *t. 224.* 1790; Meisn. in DC. Prodr. **2**: 59. 1825, **14**: 601. 1857; Royle, Illus. Himal. Bot. **1**: 173. 1835, **2**: *t. 36.* 1839; Meisn. Pl. Vasc. Gen. 73. 1836; Arnott in Lindl. Nat. Syst. ed. 2, 442. 1836; Hook. Ic. **1**: *t. 6.* 1837; Endl. Gen. 333. 1837; Roxb. & Colebrooke in Trans. Linn. Soc. **21**: 199, *t. 21.* 1854.

Agallochum Rumph. Herb. Amb. **2**: 34, *t. 10.* 1741; Lam. Encycl. **1**: 47. 1783.
Ophiospermum Reichb. Consp. 82. 1828.
Ophiospermum Lour. Fl. Cochinch. 280. 1790; Meisn. in DC. Prodr. **2**: 59. 1825.
Decaisnella O. Kuntze, Rev. Gen. Pl. **2**: 584. 1891.

According to Roxburgh and Colebrooke, the flowers are incomplete; calyx campanulate, 5-cleft; corolla none; nectary (scales) 10-leaved, alternate with stamens; capsules superior, 2-celled, 2-valved; seed solitary; embryo inversed, without perisperm.

Distribution of the genus: Northeastern India, southern China, Hongkong, Malaysia to New Guinea.

[5] J. D. Hooker, Fl. Brit. Ind. **5**: 192. 1890.

Philippine Species

Aquilaria acuminata (Merr.) comb. nov.

Gyrinopsis acuminata Merr. in Philip. Jour. Sci. Bot. 17: 294. 1920, Enum. Philip. Fl. Pl. 3: 130. 1923.

Dinagat Island: Surigao Province; *Bur. Sci. 35158 Ramos and Pascasio* (type — flowering), May 13, 1919, at low altitude. Bucas Grande Island: Surigao Province, *Bur. Sci. 35055 Ramos and Pascasio* (fruiting), June 11, 1919, at low altitude.

Aquilaria apiculata Merr. in Philip. Jour. Sci. 20: 411. 1922, Enum. Philip. Fl. Pl. 3: 130. 1923.

Mindanao: Bukidnon Province, *Bur. Sci. 38601 Ramos and Edaño* (type), in dry forests, altitude 1100 m.

Aquilaria brachyantha (Merr.) H. Hallier in Med. Rijks Herb. 44: 16. 1922.

Gyrinopsis brachyantha Merr. in Philip. Jour. Sci. Bot. 7: 313. 1912, Interpret. Herb. Amb. 380. 1917, Enum. Philip. Fl. Pl. 3: 130. 1923; Elmer, Leafl. Philip. Bot. 5: 1629. 1913.

Cortex filarius Rumph. Herb. Amb. Auct.: 13. 1755.

Luzon: Cagayan Province, Abulug River, *Bur. Sci. 13862 Ramos* (type), Jan. 28, 1912, *For. Bur. 17220, 19562 Convocar*, Jan. 25, 1912. Alabat: Tayabas Province, *Bur. Sci. 48136 Ramos and Edaño,* Oct. 8, 1926, *Bur. Sci. 48220 Ramos and Edaño,* Sept. 21, 1926. Borneo, Amboina.

The calyx is campanulate.

Aquilaria malaccensis Lam. Encycl. 1: 49. 1783; Gamble in Jour. As. Soc. Beng. 75^2: 264. 1912; Merr. in Philip. Jour. Sci. Bot. 10: 44. 1915, Enum. Philip. Fl. Pl. 3: 130. 1923.

Aquilaria secundaria Meisn. in DC. Prodr. 2: 59. 1825.

Aquilaria ovata Cav. Diss. 377, *t. 224.* 1790.

Agallochum secundarium (*coinamense* et *malaccense*) Rumph. Herb. Amb. 2: 34, 35, *t. 10.* 1741.

Luzon: Camarines Prov., Salauigan, *For. Bur. 21452 Alvarez*, May 21, 1914. Malay Peninsula, Sumatra, Siam.

Excluded Species

Aquilaria pentandra Blanco, Fl. Filip., ed. 1, 373. 1837. Philippines.

Extra-Philippine Species

Aquilaria Agallocha Roxb. Hort. Beng. 33. 1814, Fl. Ind. ed. 2. 2: 422. 1832.

Agallochum secundarium Calambac Rumph. Herb. Amb. 2: 34. 1741.

Bengal, Assam.

Aquilaria Baillonii Pierre ex Lecomte, Fl. Gén. Indo-Chine, 5: 179. 1915. Indo-China: Cambodia.

Aquilaria Crassna Pierre ex Lecomte in Bull. Soc. Bot. France, 61: 411. 1915. Indo-China: Cambodia.

Aquilaria hirta Ridley in Jour. Roy. As. Soc. S. Br. 35: 78. 1901. Malay Peninsula.

Aquilaria khasiana H. Hallier in Med. Rijks Herb. 44: 18. 1922. India.

Aquilaria microcarpa Baill. in Adansonia 11: 304. 1875. Sarawak, West Borneo.

Aquilaria Moszkowskii Gilg in Notizbl. Bot. Gart. Berlin, 5: 84. 1908. Sumatra.

Aquilaria Ophispermum Poir. in Dict. Sci. Nat. 18: 161. 1820.

Aquilaria chinensis Spreng. Syst. 2: 356. 1825.

China.

Aquilaria rostrata Ridley, Fl. Malay Penin. 3: 148. 1924. Malay Peninsula.

Aquilaria sinensis (Lour.) Merr. in Philip. Jour. Sci. **15:** 248. 1919.
Ophispermum sinense Lour. Fl. Cochinch. 280. 1790.
Aquilaria grandiflora Benth. Fl. Hongk. 297. 1861.
China.

Gyrinops Gaertner

Gyrinops Gaertn. Fruct. **2:** 276, *t. 140*. 1791; Meisn. in DC. Prodr. **2:** 60. 1825, **14:** 602. 1857; Arnott in Lindl. Nat. Syst. ed. 2, 442. 1836; Meisn. Pl. Vasc. Gen. 73. 1836; Hook. Ic. **1:** *t. 5*. 1837; Endl. Gen. 333. 1837.

Perianth tubular, cylindric, slender; stamens 5, arranged in a row; nectarial scales inserted above the stamens, connate in a ring; other features resembling *Aquilaria*.

The genus *Gyrinops* is based on the type of *Gyrinops Walla* Gaertn. Five species are known today under this genus. Domke[6] reduced three species of *Brachythalamus* to *Gyrinops*. The latter genus is distinct from *Aquilaria* and *Gyrinopsis* in having only five stamens. Domke described another species, *G. Ledermannii,* from New Guinea. Hallier[7] reduced all the species of *Gyrinops* to *Aquilaria,* with which I do not agree.

Extra-Philippine Species[8]

Gyrinops caudatus (Gilg) Domke in Notizbl. Bot. Gart. Berlin, **11:** 349. 1932.
Brachythalamus caudatus Gilg in Bot. Jahrb. **28:** 146. 1900.
New Guinea.

Gyrinops Ledermannii Domke in Notizbl. Bot. Gart. Berlin, **11:** 349. 1932.
New Guinea.

Gyrinops moluccana (Miq.) comb. nov.
Lachnolepis moluccana Miq. in Ann. Mus. Bot. Lugd.-Bat. **1:** 132. 1863.
Aquilaria moluccana (Miq.) H. Hallier in Med. Rijks Herb. **44:** 19. 1922.
Moluccas.

Gyrinops podocarpus (Gilg) Domke in Notizbl. Bot. Gart. Berlin, **11:** 349. 1932.
Brachythalamus podocarpus Gilg in Bot. Jahrb. **28:** 146. 1900.
Aquilaria podocarpa H. Hallier in Med. Rijks Herb. **44:** 19. 1922.
New Guinea.

Gyrinops Versteegii (Gilg) Domke in Notizbl. Bot. Gart. Berlin, **11:** 349. 1932.
Brachythalamus Versteegii Gilg in Nova Guinea, **8:** 410. 1910.
Aquilaria Versteegii H. Hallier in Med. Rijks Herb. **44:** 19. 1922.
New Guinea.

Brachythalamus Versteegii Gilg is the type of the genus *Brachythalamus*.

Gyrinops Walla Gaertn. Fruct. **2:** 276, *t. 140*. 1791; Meisn. in DC. Prodr. **2:** 60. 1825, **14:** 603. 1857; Hook. Ic. **1:** *t. 5*. 1837.
Ceylon.

Gyrinopsis Decaisne

Gyrinopsis Decaisne in Ann. Sci. Nat. Bot. II. **19:** 41, *t. 1, fig. B*. 1843, Bot. Zeit.

[6] Domke in Notizbl. Bot. Gart. Berlin, **11:** 349. 1932.

[7] H. Hallier in Med. Rijks Herb. **44:** 15–20. 1922.

[8] All species of *Gyrinops* herein included are extra-Philippine. The genus is not represented in the Philippines.

2: 599. 1844; Endl. Gen. Pl. Suppl. III, 65. 1843; Walp. Repert. 5: 410. 1845; Meisn. in DC. Prodr. 14: 602. 1857; Lemée, Dict. Desc. Syn. Gen. Pl. Phan. 3: 404. 1931.

The genus *Gyrinopsis* is based on *G. Cumingiana,* described from a Philippine specimen, *Cuming 1617*. The genus has previously been reported only from the Philippines, but apparently it occurs also in Borneo and Amboina.

The perianth is slender and cylindric. There are 10 sessile stamens arranged in two rows, one below the other, unequal, the five alternating smaller. There are 10 scales, alternating with the stamens or below the stamens. The fruit develops from the side of the perianth-tube. The seeds are without umbilical cord.

PHILIPPINE SPECIES

Gyrinopsis citrinaecarpa Elmer, Leafl. Philip. Bot. 5: 1631. 1913; Merr. Enum. Philip. Fl. Pl. 3: 130. 1923.

Aquilaria citrinaecarpa (Elmer) H. Hallier in Med. Rijks Herb. 44: 18. 1922.

MINDANAO: Agusan Province, Cabadbaran (Mt. Urdaneta), *Elmer 13566*, Aug., 1912, on forested ridges, altitude about 1200 m.

Gyrinopsis Cumingiana Decne. in Ann. Sci. Nat. Bot. II. 19: 41, *t. 1, fig. B.* 1843, Bot. Zeit. 2: 599. 1844; Walp. Repert. 5: 410. 1845; Miq. Fl. Ind. Bat. 1^1: 883. 1857; Meisn. in DC. Prodr. 14: 603. 1857; F.-Vill. Novis. App. 183. 1880; Vidal, Phan. Cuming. Philip. 140. 1885, Rev. Pl. Vasc. Filip. 230. 1886; Merr. in Philip. Bur. For. Bull. 1: 41. 1903, Enum. Philip. Fl. Pl. 3: 131. 1923; Elmer, Leafl. Philip. Bot. 5: 1629. 1913.

Gyrinopsis Cumingiana Decne. var. *pubescens* Elmer, Leafl. Philip. Bot. 5: 1629. 1913; Merr. Enum. Philip. Fl. Pl. 3: 131. 1923.

Aquilaria Cumingiana (Decne.) H. Hallier in Med. Rijks Herb. 44: 17. 1922.

Aquilaria decemcostata H. Hallier in Med. Rijks Herb. 44: 17. 1922.

PHILIPPINES: *Cuming 1617* (TYPE). LUZON (Nueva Ecija, Bulacan, Tayabas, Laguna, Camarines, Albay), CATANDUANES, SAMAR, SIBUYAN, LEYTE, PANAY, MINDANAO, JOLO. In primary forests at low and medium altitudes. Celebes.

Local names: *Alahan* (Tag.); *bago* (Mbo.); *binukat* (Ak., Bis.); *butlo* (Neg.); *dalakit* (S. L. Bis.); *Maga-an* (Tag.); *palisan* (Tag.); *pamaluian* (Bag.).

Gyrinopsis urdanetensis Elmer, Leafl. Philip. Bot. 5: 1630. 1913.

Aquilaria urdanetensis (Elmer) H. Hallier in Med. Rijks Herb. 44: 16. 1922.

MINDANAO: Agusan Province, *Elmer 14195*, *13742*, in the mossy forest on exposed ridges, altitude about 1700 m.

Local names: *Makolan* (Mbo.); *mañgod* (Mbo.).

Gyrinopsis parvifolia sp. nov.

Frutex circiter 1 m. altus, partibus junioribus subtus foliis fructibusque exceptis glabris; foliis lanceolatis vel anguste lanceolatis, utrinque attenuatis, acutis vel apice leviter acuminatis, ad 8.7 cm. longis et 2.5 cm. latis, supra glabris, subtus parce pubescentibus, nervis primariis utrinque 7–10, leviter prominentibus, petiolo ad 5 mm. longo; capsulis parce pubescentibus, ad 1.2 cm. longis, obovoideis, in siccitate rugosis; pedunculis dense pubescentibus.

Shrub about 1 m. tall (Edaño), glabrous except the growing tips, young leaves, petioles, peduncles, and capsules. Leaves small, subcoriaceous, lanceolate or narrowly lanceolate, narrowed to an acute apex and base, the

apex in some cases somewhat acutely acuminate, 4.5–8.7 cm. long, 1–2.5 cm. wide, greenish or olivaceous when dry, glabrous above, the lower surface slightly pubescent, in young unopened leaves very densely pubescent, the primary lateral nerves somewhat distinct, 7–10 on each side of the midrib, the secondary ones exceedingly numerous, very slender, densely arranged, the petioles slender, glabrous with age, otherwise pubescent, 4–5 mm. long. Perianth (in fruit) slightly pubescent, 5–6 mm. long including the lobes, the lobes 5, broadly ovate, rounded, about 1.5 mm. long. Capsules yellowish, rugose when dry, slightly pubescent, obovoid, 10–12 mm. long, 2-valved, 2-seeded (sometimes 1-seeded), more or less compressed, the seed broadly ovoid, apiculate, dark brown, glabrous, shining, smooth, 8–9 mm. long, 6.5–7 mm. wide, flat on the ventral side, the peduncles densely pubescent, very short, 1–2 mm. long.

LUZON: Camarines Sur Province, Her-it River, *Bur. Sci. 76441 Edaño* (TYPE), December 10, 1928, on forested slopes, altitude about 1000 m.

This species is closely allied to *G. urdanetensis* Elmer, from which it is distinguished by its differently shaped leaves with somewhat prominent primary lateral nerves, and its pubescent capsules.

Gyrinopsis pubifolia sp. nov.

Frutex circiter 1 m. altus, ramis et foliis supra exceptis pubescens; foliis lanceolatis, ad 18 cm. longis et 5 cm. latis, graciliter acuminatis, basi cuneatis; nervis lateralibus primariis utrinque 12–16, secundariis numerosis, dense dispositis; floribus parvis, circiter 1 cm. longis, axillaribus, fasciculatis.

Shrub about 1 m. high (fide Edaño), pubescent except the branches and older branchlets and upper surface of the leaves, the branchlets terete, brownish. Leaves lanceolate, 10–18 cm. long, 3–5 cm. wide, slenderly acuminate at apex, narrowed to the cuneate base, greenish and shining on both surfaces when dry, chartaceous, glabrous above, soft pubescent beneath, the primary lateral nerves distinguishable, 12–16 on each side of the midrib, the secondary ones numerous, very slender, somewhat obscure, the petioles pubescent, 4–7 mm. long. Inflorescence in few-flowered fascicles, sessile or very shortly peduncled (peduncles 1–1.5 mm. long). Flowers 10–15 mm. long, the pedicels very slender, pubescent, 2–3 mm. long, the tube slender, slightly pubescent; stamens 10 arranged in a single row near the throat, the filaments nearly sessile, ciliate, the anthers about 1.5 mm. long, the scales 10, densely ciliate; ovary densely pubescent, oblong-obovoid, narrowed downward, the style sessile, the stigma capitate.

CATANDUANES: Mt. Abucay, *Bur. Sci. 75314 Edaño* (TYPE), September 11, 1928, on summit, altitude about 1600 m.

A species doubtless allied to *G. Cumingiana* Decne., differing conspicuously in its pubescent leaves and smaller flowers. It differs from *Elmer 10981* (*G. Cumingiana* Decne. var. *pubescens* Elmer) in the color, shape, and size of the leaves.

EXTRA-PHILIPPINE SPECIES

Gyrinopsis grandifolia (Domke) comb. nov.

Aquilaria grandifolia Domke in Notizbl. Bot. Gart. Berlin **11**: 348. 1932.

I have not seen the type, which is from Sumatra. But based on the

description (calyx-tube more or less cylindrical, about 7 mm. long and 2 mm. in diameter; scales 10; stamens 10, subsessile or the filaments 0.2–0.8 mm. long), there seems no doubt that it is a *Gyrinopsis*. The leaves are unduly large (17–27 cm. long, 6–7.5 cm. wide). The lateral nerves on both sides of the midrib are prominent, 15–25. The species, therefore, by its description, is apparently allied to *Gyrinopsis Cumingiana* Decne.

Gyrinopsis salicifolia (Ridley) comb. nov.

Gyrinops salicifolia Ridley in Trans. Linn. Soc. Bot. II. **9**: 145. 1916.

New Guinea.

Natural History Museum,
Manila.

THE LICHEN FLORA OF THE PHILIPPINES

ALBERT W. HERRE

THE LICHEN flora of the Philippines is one of great interest. This, however, is only to be expected from the geographical position of that marvellous archipelago, which is really a northern spur of the East Indies. While the Philippines lie entirely in the monsoon area of the rainy tropics, there is a great variety of ecological conditions within their limits. From the rocky and storm-swept Batanes Islands at the extreme north not far from Formosa, to the Sibutu Islands well down on the east coast of Borneo, there is a range of climates and habitats that ensures a lichen flora that is relatively as large and diversified as that of the flowering plants. The altitudinal range of the many high peaks, reaching up to almost ten thousand feet, adds greatly to the variety and ensures a well represented boreal element in the lichen flora.

The Philippine lichen flora long remained almost unknown. The lichens of Indo-China, Java, Labuan, New Caledonia, and other regions not too remote from the Philippines were more or less well known before 1890.

So far as can be ascertained, the only lichens known from the Philippines before 1909 were those discussed in the following few paragraphs. *Sticta tomentosa* Ach. was collected in 1830 by the distinguished German botanist Meyen; on his trip around the world Meyen was the guest for a month of the noted Paul de la Gironnière at his great estate, Jala Jala, on the north shore of Laguna de Bay. Charles Gaudichaud, a celebrated French botanist, visited Manila on the Bonite in 1836 and collected five lichens: *Ramalina furcellata* (Montagne) A. Zahlbr. var. *torulosa* (Nyl.); *Physcidia callopis* (Meyen & Flot.) Müll. Arg.; *Ocellularia concolor* Meyen & Flot. (these three are not mentioned by Wainio and the two following have not been taken since Gaudichaud collected them); *Graphis persicina* Meyen & Flot.; *Opegrapha prosodea* Ach. var. *sclerocarpa* (Meyen & Flot.) Wainio.

The unrivalled English collector, Hugh Cuming, was in the Philippines from 1836 to 1839 and traveled over a large part of the islands. Although his real interest was in conchology, he collected in several other lines of natural history and secured 30 sets of botanical specimens. Among these were 25 species of lichens, as follows:

Trypethelium anomalum Ach.; *Trypethelium areolatum* Montagne; *Laurera Cumingi* Mont.; *Phylloporina rufula* (Krempelh.) Müll. Arg. var. *rhodoplaca* Müll. Arg.; *Graphis tenella* Ach.; *Graphina Achari* (Fée) Müll. Arg.; *Graphina Babingtoni* (Mont.) A. Zahlbr.; *Phaeographis chrysenteron* (Mont.) Müll. Arg.; *Phaeo-*

graphis flexuosa (Nyl.) Müll. Arg.; *Sarcographa Leprieuri* (Mont.) Müll. Arg.; *Ocellularia Berkeleyana* (Mont.) A. Zahlbr.; *Pannaria lurida* (Mont.) Nyl.; *Pannaria mariana* (E. Fr.) Müll. Arg.; *Coccocarpia pellita* (Lam.) Müll. Arg. var. *incisa* (Pers.) Müll. Arg.; *Physma bursinum* (Ach.) Müll. Arg.; *Leptogium phyllocarpum* (Pers.) Mont.; *Leptogium tremelloides* (Linn. fil.) S. F. Gray, var. *azureum* (Swartz) Nyl.; *Sticta argyracea* Del. var. *aspera* (Laur.) Krempelh.; *Sticta sinuosa* Persoon; *Lecidea piperis* (Spreng.) Nyl.; *Stereocaulon ramulosum* Ach.; *Parmelia relicina* (E. Fries); *Ramalina vittata* Nyl.; *Pyxine sorediata* E. Fries; *Physcia applanata* (Fée) A. Zahlbr.

Of the 25 listed above, ten are not mentioned by Wainio, and a number have never been taken since Cuming obtained them. Apparently the Spanish botanists never collected a Philippine lichen. The 31 species named above were all that were known from the islands until after the Americans came. In talking to Dr. Alexander Zahlbruckner, in 1907, I was urged almost every day to go to the Philippines to collect and study lichens. Always he would say "Aber, es ist eine ganze neue Welt." He believed it was the last considerable area left with a large and diversified lichen flora which was quite unknown.

With the beginning of scientific work by Americans in 1902, the botanists of the Bureau of Science and Bureau of Forestry and their native assistants began to take an active interest in collecting lichens as well as ferns and flowering plants. The botanists most ardent in collecting lichens were E. D. Merrill, C. F. Baker, Mrs. Mary Strong Clemens, E. B. Copeland, H. M. Curran, A. D. E. Elmer, F. W. Foxworthy, and C. B. Robinson. Equally keen in obtaining lichens was the ornithologist R. C. McGregor, while C. M. Weber also collected many. Native assistants who paid special attention to lichens were G. Edaño, Eugenio Fénix, L. Mangubat, and above all M. Ramos. Besides these, other Americans and Filipinos contributed lichens to the herbarium of the Bureau of Science.

The large amount of material collected by them was sent by Dr. E. D. Merrill to the noted lichenologist, Dr. E. A. Wainio, of Helsingfors, Finland. His results were published in four papers, from 1909 to 1923 (2–5). With the appearance of this work of nearly 500 pages of descriptive text, the broad outlines of the Philippines lichen flora were at last set forth. Wainio listed 92 genera and 680 species, besides many varieties, some of them really worthy of specific rank. Adding eleven species collected between 1830 and 1840 and not mentioned by Wainio, as he lacked material for study, 691 species are thus far recorded from the Philippines. Of the 680 species given by Wainio, 441 or 64.85% are new. This is an amazing proportion and well supports Zahlbruckner's statement.

This great ratio of endemism is actually more apparent than real. There is no question but that, when intensive lichen collecting is done in other parts of the oriental tropics from the mainland and Sumatra to New Guinea and the Solomons, the proportion will change. Wainio's

new species will be found in these other regions, just as many supposedly endemic California lichens are now known to occur in adjoining states and even in regions far away.

It is well to note that Wainio's publications are far from presenting a complete conspectus of the Philippine lichen flora. On sea cliffs occur unrecorded species of *Roccella* and other fruticose and crustaceous lichens, while the tablelands of Mindanao show earth-dwelling *Lecideae* and other undescribed lichens. Strange Graphidaceae occur on mossy rocks in the mountain gorges above Dumaguete, and on trees in various regions. Critical examination of rocks would make possible large additions to the lichen flora. In the past rock lichens have either escaped observation or else collectors have not been prepared to remove them from the substratum. It is safe to assume that over 800 species of lichens will ultimately be known from the Philippines. Intensive collecting in the Batanes Islands and on the limestone cliffs and peaks of Palawan should raise the list nearly to that figure. However, optimism must be tempered by a recognition of the destruction by man and its impact on the lichen flora. The rarities obtained by Gaudichaud and Cuming at Manila may be extinct, so great have been the changes during the past century. The conversion of forests to cogonales, and the terrific erosion following caiñgan culture on steep hillsides, may well have brought other lichens to extinction.

The composition of the Philippine lichen flora is in marked contrast to that of the United States or Europe. Naturally it is much like that of the rest of the oriental rainy tropics. But it also has species previously known only from Brazil, Colombia, Peru, the West Indies, and other American localities. Such instances merely indicate how little collecting has been done in the intervening regions. The family best represented is the Graphidaceae. *Graphis* has 39 species, of which 19 are new in Wainio's work, *Graphina* has 33 with 25 new, *Phaeographis* has 26 of which 19 are new, and *Phaeographina* 12 species and eight new. This is a total of 110 species in *Graphis* and its very close allies, which Wainio considered but subgenera.

A botanist new to the Philippines is usually disappointed in the lichen flora. The cities, like those elsewhere, are poor places for lichens, and the interminable rice paddies and sugar cane fields are no better for lichens than the corn and wheat fields of the middle west. Coconut groves are better, but collecting is very poor in the mountain rain forests or the vast jungles of the upper Agusan valley. The pale spots which often cover the trunks of trees in such places are lichens, but their thallus is defective and they never fruit, owing to the excessive moisture and twilight shades of the forest. Mosses, liverworts and ferns thrive much better in such locations. If one is able to leave the gloom below and gain access to the tree tops far above he will find lichens abundant. On the edge of the forest

beside clearings, especially where jakfruit occurs, crustaceous and foliaceous bark lichens are profuse and in great variety. An examination of the leaves of shrubs and trees reveals a wealth of epiphyllous species, often in bewildering variety to the North American or European. No doubt there are numerous unknown leaf lichens awaiting discovery in Philippine forests.

At the same time the islands have lichens well known in Europe and the United States, and when one is encountered it is like meeting an old friend in a place where all is strange. Most of them occur in the mountains or on plateaus, at elevations from 2,000 to over 9,000 feet. Among them are the following: *Microphiale diluta* (Pers.) A. Zahlbr.; *Microphiale lutea* (Dicks.) A. Zahlbr.; *Leptogium azureum* (Sw.) Nyl.; *Pannaria leucosticta* Tuck.; *Pannaria rubiginosa* (Thunb.) Del.; *Sticta aurata* (Ach.); *Sticta crocata* (L.) Ach.; *Peltigera polydactyla* (Neck.) Hoffm.; *Cladonia sylvatica* (L.) Rabenh.; *Cladonia Floerkeana* (E. Fr.) Sommerf.; *Cladonia bacillaris* Nyl.; *Cladonia coccifera* (L.) Willd.; *Cladonia didyma* (Fée) Wainio; *Cladonia furcata* (Huds.) Schrader; *Cladonia squamosa* (Scop.) Hoffm.; *Cladonia gracilis* (L.) Willd; *Cladonia pityrea* (Floerke) E. Fr.; *Cladonia verticillata* Hoffm.; *Pertusaria velata* (Turn.) Nyl.; *Lecanora subfusca* (L.) Ach.; *Haematomma puniceum* (Ach.) Mass.; *Parmelia perlata* (L.) Ach.; *Parmelia cetrata* Ach.; *Usnea florida* (L.) Web.; *Usnea longissima* Ach.; *Usnea trichodea* Ach.; *Physcia picta* (Swartz) Nyl.; *Anaptychia hypoleuca* (Mühlb.) Mass.; *Anaptychia leucomelaena* (L.) Wainio; *Anaptychia speciosa* (Wulf.) Mass. This does not complete the list, and we may expect it to be much extended when the Batanes Islands and the rocks of the high mountains have been thoroughly explored.

The extensive lichen collections of the Bureau of Science, largely named by Wainio but with many named by G. K. Merrill and myself, along with the rare and valuable works on lichens which I selected for the great library, have been maliciously destroyed by Japanese soldiers. The loss to scientific workers in the Philippines is well-nigh irreparable. There is nothing left in the islands of the authoritative material on which Wainio worked so long and painstakingly, nothing with which future collections may be compared. At the request of Dr. E. D. Merrill I prepared sets of Philippine lichens from material examined and named by Dr. Wainio or G. K. Merrill. These sets were distributed by Dr. Merrill to the principal herbaria of the world. Some of these herbaria, as at Berlin, were destroyed during the war, but most of them are intact. These sets contained duplicates, often many, wherever the material permitted. I suggest that it would be a graceful act and an exemplar of true scientific spirit for the curators of the various herbaria to go through these sets of Philippine lichens. From them they can undoubtedly select duplicates of well represented species which can be spared for the purpose of helping rebuild botanical activities in the Philippines.

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NATURAL HISTORY MUSEUM,
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OBSERVATIONS ON SOME SHRUBBY ADESMIAE OF CENTRAL CHILE

C. Skottsberg

With two text-figures

In the dry chaparral country south of Coquimbo a tall *Adesmia* is one of the predominant shrubs; nevertheless I found some difficulty in naming it, because it did not seem to fit *A. arborea* Bert. ex Colla or *A. microphylla* Hook. & Arn., the shrubby species supposed to occur in this region. A study of the literature and of herbarium specimens showed that there has been and still is some confusion about *A. arborea* and its relatives, which made me look a little closer into the matter. The result is communicated below.

Adesmia arborea of Bertero and of Colla

I quote Colla's description in full (4, p. 58):

"*A. arborea* (Berter. in Merc. Chil. 12. p. 557 sine descriptione); caule frutescente ramisque glanduloso-scabris, foliis fasciculatis 7–10-iugis, foliolis subsessilibus ovato-oblongis ciliatis, pedunculis axillaribus 1-floris folio brevioribus, leguminis longe barbatis (flores flavi)" Nob. Habitat in fruticetis collium apric. *Quillota*, cult. in h. ripul. e seminibus missis ab Auctore; stamina in hac stirpe 5–10, setae leguminum barbato-plumosae versicolores; ergo in sect. I (*Chaetotricha* DC. l. c.) collocanda."

Walpers (11, p. 729) quotes "Mercurio chilense" XII. 559 and Colla's paper. I have not had access to Bertero's original paper, but only to Dr. Ruschenberger's English translation (1), where we find, on p. 67 under *Adesmia*: "The *Palhuen* which I have named *A. arborea,* a pretty shrub which is found in the stony and arid situations about hills approaches the *Zuccagnia punctata.* Cavanilles. Its foliage, the number and color of its flowers, and above all its pods, clothed with very long and different colored hairs, make it interesting in English gardens. The other species are all herbaceous. . . ." From this we may conclude that Bertero recognized only *one* arborescent species. According to Clos (3, p. 196), *Palhuen* is the common name for *A. microphylla* Hook. & Arn., but it is also used for what he describes as *A. arborea,* together with *Espinillo,* which, as we shall see presently, is the name given by Bertero for *A. microphylla,* distributed by him as *A. arborea.*

Whether Colla drew his description from specimens he received or only from those he raised from seeds, I do not know. In Herb. Stockholm is a specimen of Bertero with two labels: (a) testified as written by Bertero:

"*761*[1] *Adesmia arborea Bertero vulgo espinillo. In fruticetis lapidosis collium Quillota (Chile) 1819 8 br. 9 mbr.*"; (b) *Adesmia arborea. microphylla Hook.* (added later). This specimen, which forms part of the type material of *A. arborea* Bert., is *eglandulose,* has 4–6 pairs of obovate-orbicular, very small leaflets, and racemose flowers supported by minute bracts. It cannot have anything to do with Colla's *A. arborea* but it is identical with *A. microphylla* of Hooker & Arnott. To judge from a note (5, p. 55), these authors came to the same result: "Our *Adesmia microphylla* we have received from Mr. Mathews as the *arborea* of Bertero's MSS. But this plant of Bertero M. Guillemin is disposed to refer to *Zuccagnia punctata* of Cavanilles." This, as far as I can see, is an impossible suggestion. Bertero was familiar with Cavanilles' work, and could not very well have mistaken *Zuccagnia punctata,* well described and figured by Cavanilles (2, p. 2, *pl. 403*) for an *Adesmia.* On the other hand, it is easy to show that Bertero's *A. arborea* was a mixture.

Ademsia arborea of Clos and Reiche

Clos (3, p. 192) divides *Adesmia* § V, Plantas frutescentes y espinosas, into two groups: 1. Flores no arracimadas, and 2. Flores dispuestas en rácimos. In group 1 the branches carry numerous more or less semi-globular dwarf shoots with fasciculate leaves surrounding a few axillary flowers; in the second group these shoots, after a few very short internodes, become prolonged, forming a raceme as a rule terminated by a spine. To the first group *A. arborea* Bert. is referred, to the second *A. microphylla.* Clos gives a detailed description of the former, which is a tree, 6–7 feet high, eglandulose in all parts; the branches, which end in 2- or 3-furcate spines, are provided with dwarf shoots in the shape of tubercles carrying leaves and flowers; leaves canescent, with 3 or 4 pairs of small oval leaflets; calyx-teeth narrow, acute, of the same length as the tube. It grows in the provinces of Colchagua and Santiago, north to Coquimbo. Clos adds (p. 195): "Creemos que la *A. arborea* de Colla deberia mas bien unirse á la *A. glutinosa,* puesto que está descrita como glandulosa y nada se dice de sus espinas, que son muy raras en esta última especie." This is, however, not very probable, because *A. glutinosa* belongs to the second group of Clos, while Colla's *A. arborea* falls within the first. Clos continues: "Nuestra planta es por cierto la *A. arborea* de Bertero, de la que tenemos á la vista los ejemplares recojidos y marcados por el mismo." Consequently, Bertero must have distributed two different species under the name of *A. arborea,* one of which is equal to *A. microphylla* Hook. & Arn., the other differing from Colla's *A. arborea* in lacking all glands and in having 3 or 4 pairs of leaflets instead of 7–10. Unfortunately, I have not had an opportunity to examine Colla's type. That *A. arborea* Bert. is a mixture was pointed out by Steudel (10, p. 27). Under *A. microphylla* we find as a synonym "A. arborea. *Bert.* hrb. (ex parte nr. 763 non nr. 5)," whereas no. 5 is

[1] Or *763?*; the last figure is indistinct.

called "A. Berteroniana. *Steud.* A. arborea *Berter* (ex parte nr. 5. non 763)," and under *A. arborea* Bert. we find "A. Berteroniana, microphylla." Colla is not mentioned by Steudel. Index Kewensis retains *A. arborea* Bert. and refers *A. arborea* Colla to *A. glutinosa* Hook. & Arn. without a query.

Philippi (6, p. 48) lists *A. arborea* Bert. Mem. Tor. XXXVII. 59, where, as we have seen, Colla is the author; besides, he idenitifies an "arborea Colla ubi?" with *A. viscosa* Gill., a very different plant.

Reiche's *Patagonium arboreum* (Bert.) (8, p. 120), "Adesmia arborea Bert. Gay II páj. 194", is identical with Clos' and the description is an abbreviated translation of his. He does not quote Colla, but under *Patagonium glutinosum* (Hook. & Arn.) we find as a synonym "*Medicago arborea* Colla." As far as I am aware, Colla never described such a species. Probably Reiche has copied Philippi (6, p. 49), who puts "Medicago arborea Colla" as a synonym of *A. glutinosa.* The distribution of *A. arborea* is according to Reiche from Coquimbo to Linares, in sterile hills, but not in the littoral zone, but he also lists it from Valparaiso (4, p. 196), rather a doubtful record.

I have seen two collections clearly belonging to *A. arborea* of Clos and Reiche:

(1) "*Adesmia arborea* Bert. Chile centralis, Prov. Colchagua, ad Baños de Cauquenes, 28. VIII. 1896. *P. Dusén*" (S). Figs. 1, 2.

Morphology as described. Leaves 15–20 mm. long, including the petiolar half of the rachis, rather densely canescent, with 3 or 4 (very rarely 5) pairs of leaflets 2–3 × 1–1.5 mm., these elliptic-obovate, in some cases minutely apiculate. Calyx densely canescent, 4.5–5 mm. long, including teeth of 2–2.5 mm.; standard with a glabrous limb 5–6 × 7–8 mm. and a boat-shaped claw 1.7–2.1 mm. long; wings with limb 5.7–6.1 × 3.5–3.8 mm. and claw 2.4–2.7 mm. long; keel with limb 5–5.2 × 2.8–3.7 mm. and a claw of 2.5–2.7 mm. Stamens apparently anomalous in most flowers. Ovary 5-jointed, densely hirsute along edges, the sides of joints with numerous glandular appendices, becoming greatly lengthened and plumose in the developed pod. Flowers yellow with veins marked with reddish brown.

(2) "*Adesmia arborea* Bert. Nom. vulg. *Palhuén.* Prov. Santiago, alt. 1450 m. X. 1931. *C. Grandjot.*" (S). Figs. 3, 4, 25.

Very like the former. Leaves to 20 mm. long, generally 3- but sometimes 4-jugate, the leaflets linear to linear-spatulate, obtuse and more or less distinctly apiculate, 3-5 × 0.7–1.7 mm., puberulous. Calyx 5–5.5 mm. long including the 2–3 mm. long linear-subulate teeth. Standard as in the former, the limb 4.5–5 × 7.8 mm., the claw 1.7–2 mm. long; limb of wings 4.7 × 3.7 mm., the claw 3.5 mm. long; keel with limb 4.5 × 4 mm., the claw 3 mm. long. Longer stamens 8-8.5 mm. long, the shorter ones 7–7.5 mm. long. Ovary 4- or 5-jointed, as before, the style 6 mm. long. In an envelope is an almost ripe pod, but whether or not it belongs to the specimen I cannot tell. It measures 16 mm. long, with three fertile joints, their flat sides adorned by plumose setae 7–8 mm. long. They are less

numerous than in *A. glutinosa*, so that the pubescent wall of the pod, which is completely hidden in this, is visible.

Adesmia arborea Bert. is a *nomen nudum*. It does not include *A. arborea* Colla, which is a dubious species, but two other species, *A. microphylla* Hook. & Arn. and *A. arborea* in the sense of Clos and Reiche. For the latter we may better take up the name *A. Berteroniana* Steud.

Adesmia microphylla Hook. & Arn. (5, p. 19, *pl. IX*)

A well-defined species, of which I have seen numerous specimens.

Described as a decumbent, intricately branched shrub; the long shoots carry much reduced, tuber-like dwarf shoots with a fascicle of leaves surrounded by the old persistent stipules. Leaves pubescent, as much as 6-jugate, the leaflets very small, orbicular. The dwarf shoots are not represented in the plate, which does not give a good idea of the morphology; the leaves are drawn as 3- or 4-jugate with mostly alternate leaflets, and in many cases they show a terminal leaflet, which I believe never develops. The flowers are borne in terminal racemes ending in a needle-pointed spine, but the plate gives no idea of the complex system of vegetative-floral branches. The short calyx-teeth are quite characteristic of *A. microphylla*. The pod is said to be 3-jointed, but all the pods figured are 4-jointed, and this seems to be the rule.

The type was collected by Menzies at Valparaiso, where *A. microphylla* seems to be common. I have examined the following specimens from the vicinity of Valparaiso:

R. A. Philippi, Pl. chil. no. *390*, Dec. 1851 (S, U); *N. J. Andersson* in 1852 (S); *W. H. Harvey* in 1856 (S); *E. Asplund* no. *3*, July 21, 1921 (S); Zapallar, n. of Valparaiso, *C. Skottsberg*, Sept. 16, 1908 (U); El Salto, n. of Valparaiso, *C. & I. Skottsberg* no. *945*, Aug. 26, 1917; Quillota, e. of Valparaiso, *Bertero* no. *761* (*763?*), in 1819 (S).

According to Reiche (8, p. 131), *A. microphylla* is distributed from Coquimbo province to Santiago and Valparaiso, and (9, p. 184) it is quoted from Frai Jorge in Coquimbo, but the frutescent *Adesmia* growing there belongs to a different species, and the records from Santiago are rather dubious.

The length of the leaves, the size and shape of the leaflets and flower-parts, etc., show a certain variation. A summary of my observations is given below.

Bertero no. *7o1* (*763?*). Leaves mostly 5-jugate, about 20 mm. long, the leaflets obovate, rarely suborbicular, (0.8–) 1–2 × 0.8–1.1 mm., thinner than in most cases. Calyx 3 mm. long, including teeth of 1 mm. I did not feel justified in sacrificing one of the very few flowers; they look exactly like those of *A. microphylla*.

Philippi no. *390*. Leaves 3- or 4-jugate, 10 mm. long, the leaflets orbicular, 1.2 × 1.2 mm. Calyx 2.5–3 mm. long, the teeth 1–1.3 × 0.8–1 mm. Standard-limb 5.3 × 8, the claw 2.9 mm. long; wing-limb 4.8 × 2.9, the claw 3 mm. long; keel-limb 4.5 × 3.2, the claw 2.5 mm. long; longer stamens 8.2, the shorter ones 5.5 mm. long.

Harvey. Leaves as in the preceding. Calyx 2.8–3 mm., the teeth 0.5–1

mm. long; standard-limb 5.5 × 7, the claw 2.8 mm. long; wing-limb 4.2 × 2.7, the claw 3 mm. long; keel-limb 4 × 3, the claw 3 mm. long; longer stamens 8.5, the shorter ones 6.2 mm. long.

N. J. Andersson. Leaves as above, the leaflets mostly shed, leaving rachis standing. Calyx 3 mm., the teeth 0.5–0.9 mm. long; standard-limb 4 × 6, the claw 2 mm. long; wing-limb 3.5 × 2, the claw 2.5 mm. long; keel-limb 4 × 2.6, the claw 2.5 mm. long; longer stamens 6.5–7, the shorter ones 5.5 mm. long.

Skottsberg, Zapallar. Leaves 10–20 mm. long, 2–5-, generally 3- or 4-jugate, the leaflets suborbicular to orbicular, very obtuse, sometimes slightly emarginate, 1.6–3.2 × 1.8–2.7 mm. Calyx 3–3.5 mm., the teeth 0.7–1 mm. long; standard-limb 9.5 × 10.5–11, the claw 3.5 mm. long; wing-limb 7.5 × 3.4, the claw 4 mm. long; keel-limb 7 × 4.6, the claw 4 mm. long; longer stamens 11, the shorter ones 9.5 mm. long. FIGS. 9, 10, 27.

Skottsberg no. *945.* Leaves 3- or 4-jugate, about 10 mm. long, the leaflets broadly ovate to orbicular, 0.9–2 × 0.9–1.5 mm., distinctly (0.2–0.4 mm.) petiolulate. Calyx 2.5–3 mm., the teeth 0.5–0.7 mm. long; standard-limb 5–6 × 7.8–9.5, the claw 2.7 mm. long; wing-limb 4.5–5 × 2.6–2.7, the claw 3–3.5 mm. long; keel-limb 4.2–4.4 × 3.3–3.5, the claw 2.7–3 mm. long; longer stamens 7.3–8.2, the shorter ones 6.3–6.5 mm. long. FIGS. 5, 6, 26.

Asplund no. *3* represents exactly the same form as *Skottsberg* no. *945.* FIGS. 7, 8.

The specimens from Zapallar differ conspicuously from the rest by their larger leaflets and flowers; leaflets of the same size are also observed in a specimen without locality, date, or name of collector (misit A. de Jussieu, 1834, S): 3- or 4-jugate, the leaflets 1.5–3.2 × 0.9–2 mm.

The ovary is, as a rule, 4-jointed, but it happens that only two or three (in some cases only one) of the joints produce seed. The setae are as much as 9 or 10 mm. long, plumose with a naked base, and the pericarp is clearly visible.

Adesmia glutinosa Hook. & Arn. (5, p. 19)

"Caule fruticoso ramoso, ramulis patentibus glanduloso-hirsutis, glutinosis spinescentibus, foliolis subtrijugis ellipticis hirsutis, racemis elongatis terminalibus simplicibus spinescentibus bracteisque linearibus glanduloso-hirsutis, leguminibus triarticulatis longissime setoso-plumosis.

"HAB. Coquimbo. — This differs from the preceding [*A. microphylla*] in its larger leaflets, longer racemes, narrower bracteae, longer pedicels, and in the viscid glands and patent hairs which clothe all the younger parts of the plant except the corolla."

Through the kindness of the Director at Kew I had occasion to see the type sheet. Framed-in is the top of a branch with a terminal inflorescence in advanced bud stage. There are very few leaves left, 10–12 mm. long, with 3 or 4 pairs of leaflets 2–2.6 × 1–1.5 mm., thick, hirsute especially beneath, and with numerous bottle-shaped glands. Stem and inflorescence, including pedicels and calyx, are covered with the same coarse pubescence and glands. The specimen is labeled "*Beechey's Voy. Adesmia glutinosa Hook. & Arn.*" in W. J. Hooker's hand, and Dr. I. M. Johnston has added

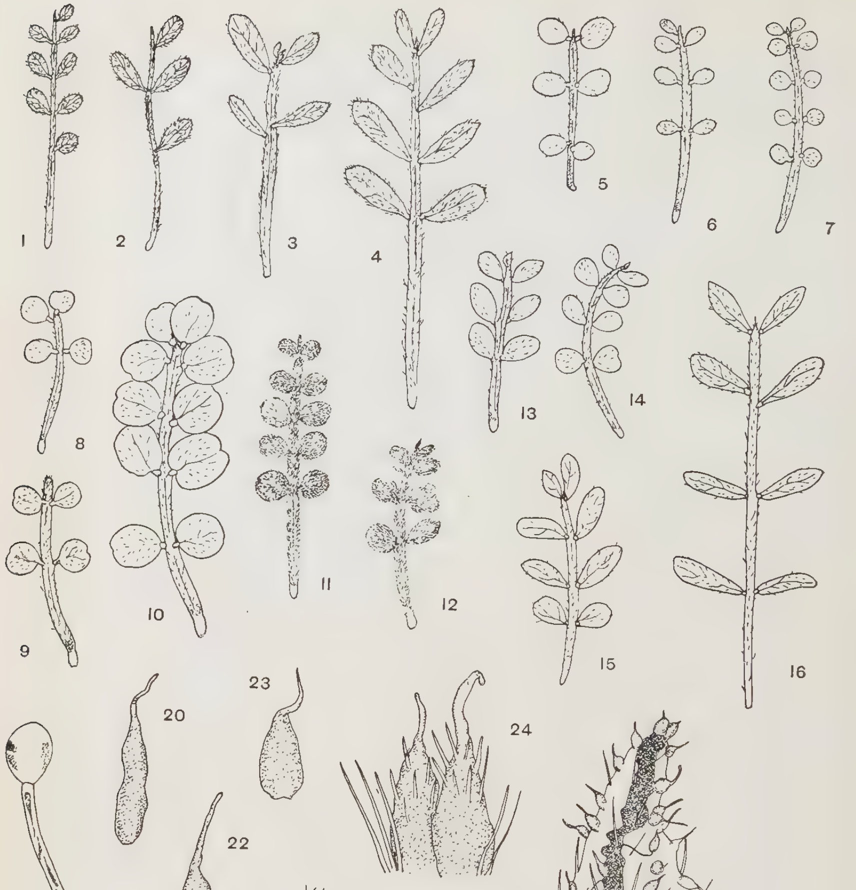

FIG. 1. 1–16. Leaves of *Adesmia* species. *1, 2. A. Berteroniana*, leg. *Dusén*; *3, 4*. id., leg. *Grandjot*. *5, 6. A. microphylla, Skottsberg* no. *945*; *7, 8*. id., *Asplund* no. *3*; *9, 10*. id., leg. *Skottsberg*, Zapallar. *11, 12. A. glutinosa, Werdermann* no. *214*; *13, 14*. id., leg. *Grandjot*. *15, 16. A. Bedwellii, Skottsberg* no. *801*. *17*. Calyx-tooth of *A. glutinosa, Werdermann* no. *214*; *18*. id., leg. *Grandjot*. *19*. Secretory gland from calyx of *Werdermann* no. *214*. *20–23*. Very young setae from pod of *A. Bedwellii, Skottsberg* no. *801*. *24*. Slightly older setae from pod of *A. microphylla, Skottsberg* no. *945*. — 1–16 × 2; 17, 18 × 20; 19–24 × 200.

"Type." The collectors are Lay and Collie. Obviously this is not the entire type material, as it lacks pods. The stump is glued to the paper, making a closer examination of the flower impossible. The calyx is about 4.5 mm. long, with acute teeth of about 2 mm.

On the same sheet are samples collected by C. Gay. The label bears in print "Herb. Mus. Paris" and "Amériq. mérid[le]. Chili," and written "Rec[u]. 1864–65. *Adesmia glutinosa Hook. Clos in Gay Fl. Chil. II, 195.*" There are numerous well developed leaves, flowers, and pods, some mature, but this material has not been used for the original description. The cortex of the old branch is dark cinnamon-colored. The leaves are 20–25 mm. long, 4- or 5- or even 6-jugate, hirsute and glandular when young, later glabrescent, with elliptic to slightly obovate, acute to very blunt leaflets averaging 3 mm. in length and 2 mm. in width (2.5–3.5 × 1.3–2.5 mm.). The pubescence and glandulosity of the stem and inflorescence are exactly as in the type, and there can be no doubt that Gay's specimen represents true *A. glutinosa;* Clos' description differs, however, in two points: the leaflets are said to be in 8–6 pairs (in the Spanish description he says 6 or 7) and only 0.5–1 mm. large; otherwise the specimens match the description perfectly. That Hooker and Arnott call the pods 3-jointed and Clos 2–7-jointed is of no importance; they are 4- or 5-jointed in Gay's specimen. It is noteworthy that in certain pods the lowermost joint is naked, whereas in others all are beset with the long, densely hairy setae which form a much thicker cover than in *A. microphylla,* so that the pericarp is completely hidden. Clos himself did not feel quite sure that his *A. glutinosa* was identical with Hooker's. The differences in the number of leaflets and pod-joints seem, however, to disappear on comparison. Another difference would be that the racemes end in a spine according to Hooker's description and type (a short and weak needle barely visible between the buds), being unarmed in Clos' plant. Whether or not the main axis terminates in a spine can not be found out without damaging the specimen, but in an undeveloped vegetative-floral branch the tip of a needle is seen.

Clos suggests that Colla's *A. arborea* is identical with *A. glutinosa,* but this is hardly possible, especially on account of "pedunculis axillaribus 1-floris folio brevioribus"; in *A. glutinosa* all the supporting leaves are reduced to bracts. Colla's plant came from the lowlands, while Clos' *A. glutinosa* is a montane species, found "en los llanos de Gantua, á 6000 pies de altura, y en otros puntos." Reiche (8, p. 126) quotes it from the Cordillera of Coquimbo at 2000 m. I suppose that the plains of Gantua are in the same range. His description is a combination of the original diagnosis and the description in Gay's Flora.

Clos mentions that he had seen specimens of *A. glutinosa* with leaves white with a dense tomentum. This form is matched by *Werdermann* no. *214,* collected in the cordillera of Río Turbio (Coquimbo) at 3000 m., Dec. 1929 (S), which may be described as follows:

It is a very spiny shrub with the cortex of the older branches deep

cinnamon-colored, and all the younger parts, including the inflorescence, very glutinous. Leaves 15–20 mm. long, densely tomentose on both faces, grayish green, generally 4- or 5-jugate, orbicular or broadly obovate, obtuse, thick and firm, 1.5–2.2 × 1.4–2.2 mm. Calyx 4.5–5 mm. long, with teeth 1.5–2 mm. long, densely glandular and glutinous; standard-limb 7 × 9, the claw 2.5 mm. long; wing-limb 5.5 × 3.6, the claw 3.5 mm. long; keel-limb 5.5–6 × 3.7 mm.; longer stamens 9–10, the shorter ones 7.5–8 mm. long; style 6.5 mm. long. This may be regarded as an alpine, more tomentose form. The pods are as in Gay's plant. FIGS. 11, 12, 17, 28.

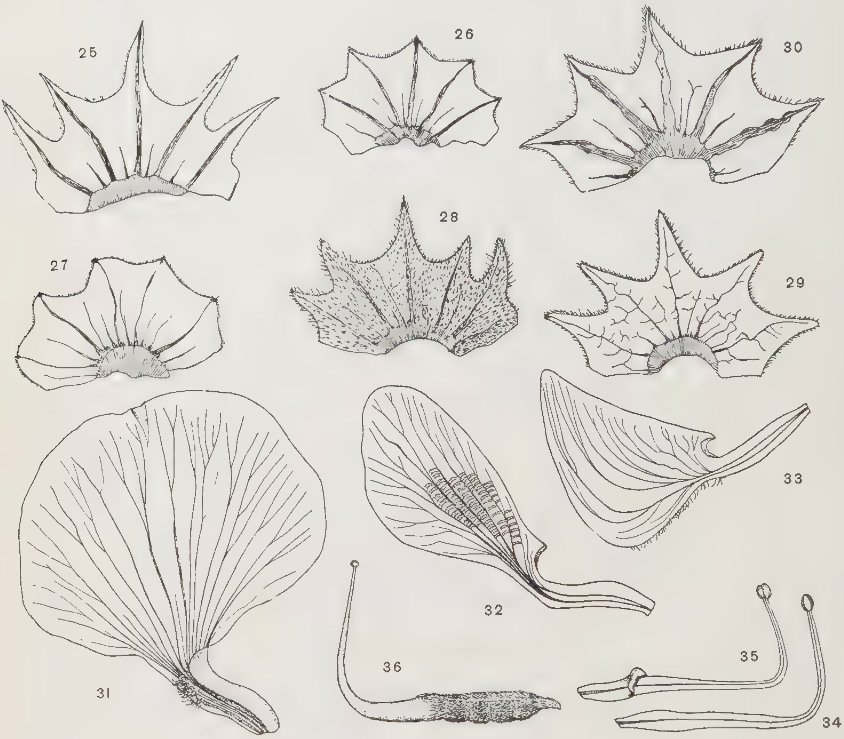

FIG. 2. 25–30. Calyces. *25. A. Berteroniana,* leg. *Grandjot. 26. A. microphylla, Skottsberg* no. *945; 27.* id., leg. *Skottsberg,* Zapallar. *28. A. glutinosa, Werdermann* no. *214; 29.* id., leg. *Grandjot. 30. A. Bedwellii, Skottsberg* no. *801.* 31–36. *A. Bedwellii: 31.* standard, *32.* wing, *33.* keel, *34.* longer stamen, *35.* shorter stamen, *36.* pistil. — All × 4.

More doubtful is another plant, collected by C. Grandjot in Sept. 1933 at Las Palmas de Pedegua, Prov. Aconcagua, alt. 650 m., and determined as *A. glutinosa*:

In general habit it resembles *A. microphylla;* the racemes and pedicels are shorter and the leaflets smaller than in *A. glutinosa,* but the glutinous pubescence, long calyx-teeth, and pod are as in the latter. Cortex dark violet-brown, more or less glossy. Leaves 10–15 mm. long, 3- or 4-, rarely

5-jugate, puberulous, dull green, the leaflets suborbicular to obovate or obcordate, 1–2 (–2.5) × 0.7–1.4 (–1.8) mm. Calyx 5–5.5 mm., the teeth 1.5–2.5 mm. long; standard-limb 7–7.3 × 9–9.5, the claw 2.7–3 mm. long; wing-limb 5.5–5.9 × 3.2–3.3, the claw 3.7–4 mm. long; keel-limb 6.7–6.9 × 4.2–4.3, the claw 3.5 mm. long; longer stamens 11, the shorter ones 9.5 mm. long; style 7.5 mm. With the material at hand I can find no good reason to separate this from *A. glutinosa*. FIGS. 13, 14, 18, 29.

Adesmia Bedwellii sp. nov.

Frutex spinescens ramosissimus usque bimetralis, cortice cinereo. Rami nodulosi, nodulis (ramis valde abbreviatis) fasciculatim foliosis, superioribus elongatis foliosis et racemigeris. Folia 15–25 mm. longa, puberula, 3–5-, vulgo 4-juga; foliola distantia, lineari-spathulata vel anguste obovata, obtusa, subsessilia, sat tenuia nervis plus minusve conspicuis, 2.5–6.5 (vulgo 3–5) mm. longa et 1–2 (vulgo 1.5) mm. lata. Racemi 2–4 cm. longi, inferne foliiferi, dein bracteiferi, apice spinescentes, rhachide parce puberula sed non glandulosa, circ. 12-flori. Bracteae triangulares, 1 mm. longae, fuscae. Flores lutei rufo-striati. Pedicellus gracillimus, puberulus et plerumque glanduloso-scaber, glandulis lageniformibus glutinosus. Calyx late campanulatus, breviter pubescens, dentibus acutis 1.5–2 mm. longis. Vexillum limbo extus pubescente, 9–10 mm. longo et 10.3–12 mm. lato, ungue 3.5–4 mm. longo superne lanato; alae limbo 7.5–8.5 mm. longo et 4–4.5 mm. lato, ungue 4.2–4.5 mm. longo; carina limbo 6.5 mm. longo et 4.3–4.5 mm. lato, margine inferiore parce lanato, ungue 3.5–3.7 mm. longo. Stamina longiora 11.5–12 mm. longa, duo breviora nectarifera 9.5–10 mm. longa, anthera 0.5 mm. longa; ovarium 5 mm. longum, stylus 6.5 mm. longus. Legumen 20–25 mm. longum 4- vel 5-articulatum, dorso tomentoso-glandulosum, latere dense setigerum, setis 8–9 mm. longis ferrugineis albo-pilosis.

CHILE: Prov. Coquimbo: Frai Jorge, alt. 200–300 m., frequens, *C. & I. Skottsberg* no. *801*, July 14, 1917 (Göteb., TYPE; S). FIGS. 15, 16, 30–36.

In his account of a visit to Frai Jorge, F. Philippi (7, p. 206) speaks of a spiny Adesmia, 1.5–2 m. high and very abundant, and adds that "although it is similar to *Adesmia arborea* Bert., the commonest kind of this vast genus near Santiago, its habit is quite different, and it may easily be a distinct species." Reiche, in his description of the vegetation of the landward slope of the Frai Jorge ridge, the same locality where no. *801* was collected, refers the shrubby *Adesmia* — and there is, as far as I know, only one kind in this district — to *A. microphylla* (9, p. 184). *Adesmia Bedwellii,* named in honor of the late Mr. F. Bedwell, owner of the Frai Jorge farm at the time of our visit, is closely related to *A. microphylla,* but differs in the much longer and narrower leaflets, glutinous pedicels, longer calyx-teeth, and larger corolla (this is, however, almost as large in the form of *A. microphylla* collected at Zapallar). From *A. glutinosa* it differs in the leaves, the lack of glands on the rachis of the raceme and calyx, and in the shorter bracts, which in *A. glutinosa* are from 1.5 to 3.5 mm. long and very narrow.

The glutinous glands in *A. glutinosa* and *A. Bedwellii* are bottle-shaped, many-celled secretory organs with a long, slender neck; in the herbarium specimens a yellow, glistening drop of the hardened resin is frequently

seen (FIG. 19). Morphologically, the setae on the pod are homologous with secretory organs, and in their young state rather like these, as seen from FIGS. 20–24.

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BOTANICAL GARDEN,
GÖTEBORG.

CENTRIFUGAL STAMENS

E. J. H. Corner

With seven text-figures

An unexpected difference among the families of dicotyledons arises from the direction in which the stamens develop. In 1857, Payer showed that, in contrast to the usual centripetal or acropetal order, there were a few families in which it was centrifugal — "l'éruption staminale est donc centrifuge," (4, p. 4). In modern works this remarkable contrast seems to have been almost entirely forgotten, yet clearly we cannot hope to understand the variations of the androecium in ignorance of it. So far as I have discovered in general reading, the following thirteen families have stamens developed centrifugally (I have placed the name of the authority in brackets):—

Actinidiaceae (Brown), Aizoaceae (Payer), Bixaceae (Corner), Cactaceae (Payer), Capparidaceae (Payer), Dilleniaceae (Payer), Hypericaceae (Payer), Loasaceae (Payer), Lecythidaceae (Mclean Thompson), Malvaceae (Payer), Paeoniaceae (Schöffel), Theaceae (Payer, Warming), Tiliaceae (Payer).

In contrast, the chief families with many centripetal stamens are:—

Annonaceae, Lauraceae, Leguminosae, Lythraceae, Magnoliaceae, Myrtaceae, Nymphaeaceae, Papaveraceae, Punicaceae, Ranunculaceae, Rosaceae.

In these, the andrœcium follows the perianth in normal sequence, whether spirally or by alternating whorls. In the centrifugal families, there is a break between the perianth and the andrœcium which is caused by the intercalation of the new stamens. Accordingly, they are not packed in parastichies but as closely as possible in centrifugal order to give the short, irregular, non-seriate rows which one finds also in the arrangement of the pores of the Polyporaceae and the spines of the Hydnaceae. We have, in fact, a new construction in which stamens arise, not in the logarithmic spirals of acropetal phyllotaxis, but on a peripherally expanding disc. In the more regular flowers of this kind, as will be mentioned, the stamens may be arranged in centrifugal whorls with a regular doubling of the number of stamens in each.

I propose to describe briefly the typical centrifugal andrœcium in the relatively massive flowers of *Wormia, Tetracera,* and *Bixa* — massive in the sense of having a large bud and wide receptacle. I will then indicate what seem to be derivative states caused by diminution in the size of the

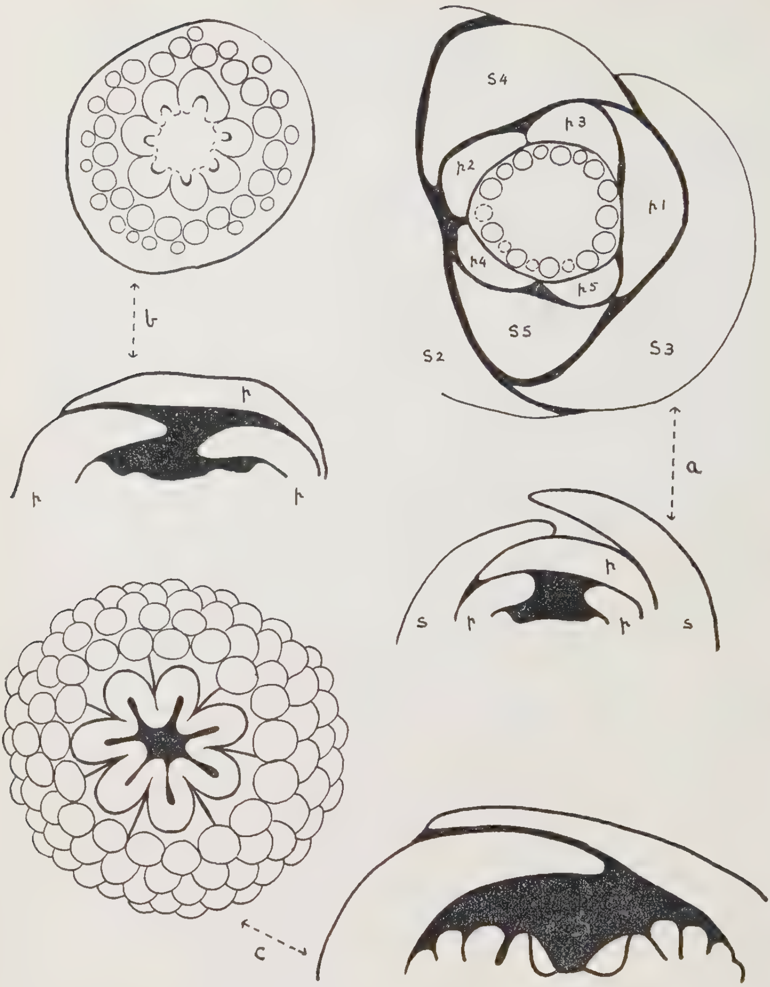

FIG. 1. *Wormia suffruticosa*: three stages in the development of the androecium, in surface-view (with the perianth cut off) and in section; *a* corresponds with *c* in *Fig. 2, b* with *d*, and *c* with *e*; s = sepals, p = petals; × ca. 45.

flower; and, finally, I will discuss the systematic or phyletic value of the feature and how a more precise notation for the andrœcium must be introduced into the floral formula. Needless to say, much more research must be done on multistaminate tropical genera before we can hope for satisfactory understanding. A mathematical theory and geometrical construction must also be worked out for centrifugal development from detailed measures of series of enlarging flower-buds: for the order of development is the opposite of that of the classical Composite-inflorescence.

THE MASSIVE CENTRIFUGAL ANDROECIUM

The massive flowers of *Dillenia, Wormia, Bixa, Gordonia, Thea, Opuntia, Saurauja,* and, probably, the Lecythidaceae show the typical features of the centrifugal, multistaminate andrœcium, thus: —

1. After the initiation of the corolla, or even before it is complete, the floral apex becomes a wide, low disc with vague angles, and its apical growth gives place abruptly to radial growth.

2. The first stamens arise in a ring of 15–21, commonly 17–18, primordia, without obvious relation to the perianth, and practically simultaneously. They may precede the carpels (*Dillenia, Wormia*) or develop just after the carpels (*Tetracera, Bixa*), in which case the first stamens alternate, more or less, with the carpels and the gynœcium and andrœcium form one centrifugal system.

3. The floral disc expands basipetally, or peripherally, between the initial staminal ring and the corolla and, on this andrœcial annulus, the other stamens (numbering 50 to several hundred) develop centrifugally in closest apposition to the preceding stamens. A tendency to develop in alternating whorls of increasing members is generally obscured by asymmetry of the floral disc.

4. The mature flower is usually perigynous with the stamens united, more or less, in a short tube developed from the basipetal enlargement of the andrœcial annulus. (In *Tetracera* the flower is secondarily hypogynous.)

Figures 1–7 will illustrate the manner of development in *Wormia, Tetracera,* and *Bixa*. The later stages, in surface-view and longitudinal section, supplement Payer's solid views of *Opuntia, Thea,* and *Gordonia.*

In *Wormia suffruticosa* there are 16–20 initial stamens around the floral apex, and the outermost, or youngest, stamens are sterile and form short ligulate staminodes (homologous with the petals of *Mesembryanthemum*); the staminodes have neither the space, nor the time, nor the food-supply (probably) to become fertile and, though there are all transitions to fertile stamens, there are no transitions to the petals as there are in the centripetally developed flowers of the Nymphaeaceae. It must be noted that the variations of the dilleniaceous andrœcium, particularly in *Hibbertia,* can be understood only by reference to its centrifugal development and the sterilization of the later stamens; it is, thus, fundamentally different from the ranalian andrœcium.

Tetracera Assa (Dilleniaceae) differs from *Wormia* in the precocity and incipient oligomery of the gynœcium. The carpels are initiated before the stamens and follow the tetramery of the perianth so that there are 7 or 8 stamens developed slightly before the others in the initial ring; the gynœcium thus induces a slight centrifugal alternation of whorls in the andrœcium, but it is soon lost as more members are inserted. The outer stamens are fertile and identical in length and appearance with the inner-

most in the open flower. The receptacle elongates shortly during the expansion of the bud and renders the flower secondarily, or indirectly, hypogynous.

In *Bixa* the gynœcium is even more precocious and appears before the

FIG. 2. *Wormia suffruticosa:* six stages (*a* — *f*) in the development of the massive flower-bud; two later stages (*g* — *h*) in the development of the androecium and gynoecium; *f* corresponds with *a* in *Fig. 3*; s = sepals, p = petals; × ca. 15.

4th and 5th petals. The floral apex is very massive when the initial ring of 17 or 18 stamens arises practically at once round the subcircular gynœcium; the ring bears no obvious geometrical relation to the perianth. In this respect, *Bixa* has the most independent andrœcium governed, apparently, merely by the spacing-relations (or bulk-ratio) between the staminal primordia and the area of the "andrœcial disc" and by the centrifugal order. All the stamens are fertile and equally long in the open flower and the only indication of its unusual development is the slight perigynous disc on the outer slope of which the stamens are inserted.

In *Saurauja subspinosa* (Actinidiaceae, 2) the andrœcium of about 50 stamens starts from a ring of 15–21. When there are only 15, five are opposite the sepals and five pairs oppose the petals, but they arise practically simultaneously. This precision in number and position, conforming with the perianth, coincides with reduction in size of the floral apex and leads to the derivative and specialised conditions in the smaller flowers which will be considered next.

The obvious interpretation of the massive centrifugal andrœcium is that the order of development has been reversed through the abrupt cessation of the apical growth of the floral bud while its radial growth continues between the gynœcium and the perianth. The generating field of the andrœcium is transformed from an acropetal cone to a centrifugal disc on which the primordia develop as enations packed as closely as their minimal initial areas admit without interference. The state is clearly derived from the massive multistaminate flower with normal acropetal sequence of stamens of modern form, for in acropetal flowers radial growth of the floral apex is regularly co-ordinated with apical growth, and both decline together; in the centrifugal flower the two are, as it were, dissociated in a curious way which should help us to analyse more clearly the growth of the stem-apex.

DERIVED CENTRIFUGAL ANDROECIA

The following four constructions seem to show how diminution in the growth of the floral bud, recognizable from the sharper angles of the floral disc after initiation of the perianth, introduces greater precision in the number and position of the stamens. For illustration, I must refer to Payer's figures.

1. *Initial whorls. Saurauja subspinosa,* just mentioned, is an instance. The floral disc, after the initiation of the perianth, becomes more or less sharply angled because it does not undergo such rapid radial expansion. On the points, or shoulders, of the disc arise five antisepalous stamens, alternating with the petals, and then ten antipetalous stamens in five pairs, slightly external to the antisepalous; after this other stamens develop as in the more massive flowers. In *Cistus* and *Helianthus* it seems that only five antipetalous stamens develop, giving an initial, regular phase of A5 + 5. In the tetramerous *Capparis spinosa* the andrœcium appears to be wholly

whorled in the centrifugal order 4 + 4 + 8 + 16 + 32 (? + 64. . . . .) so that the stamens in the mature flower appear to be arranged according to the normal centripetal, but falling, whorled phyllotaxis of the Papaveraceae.

2. *Centrifugal fascicles.* In the dilleniaceous genera *Candollea* and *Hibbertia,* after the initiation of the five petals, the pentagonal floral disc forms five antisepalous humps on each of which the stamens develop cen-

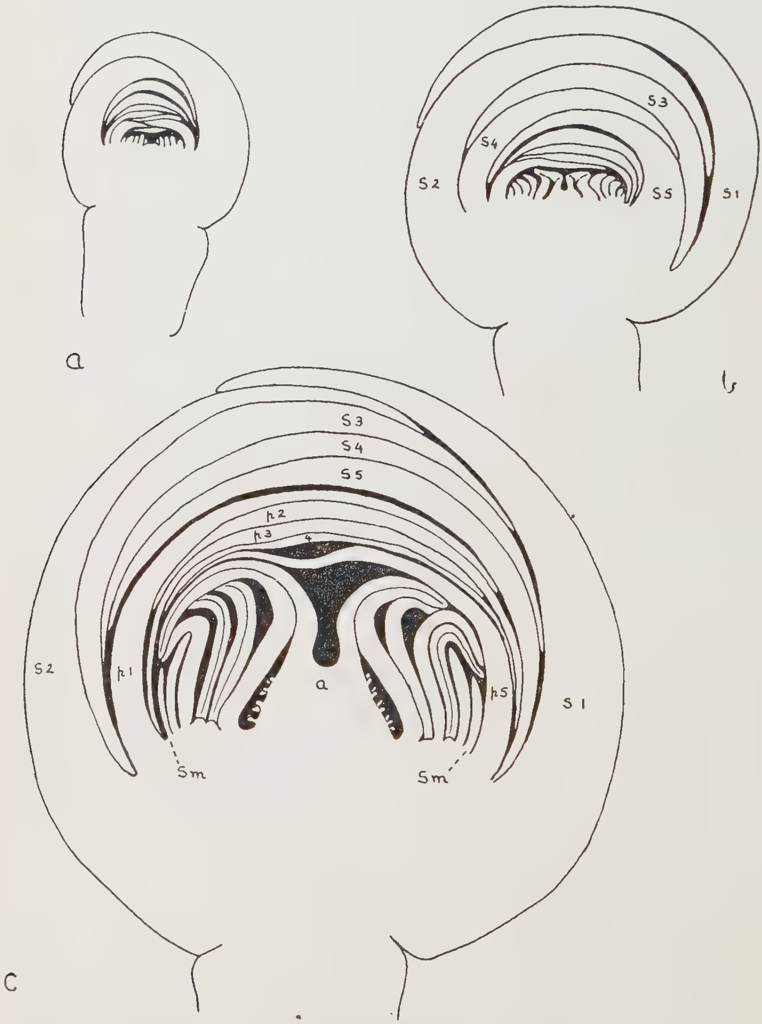

FIG. 3. *Wormia suffruticosa*: three stages in the later development of the flower, *a* corresponding with *f* in *Fig. 2*, *c* about half-grown; s = sepals, p = petals, sm = staminodes; × ca. 7.

trifugally. If the stamens are very numerous, the five groups coalesce centrifugally, but if they are relatively few (? in smaller flowers), they remain in five antisepalous clusters in the open flower. In the Hypericaceae, *Bathys prolifica* has five slight *antipetalous* humps on which the stamens develop centrifugally, but they coalesce to give a homogeneous andrœcium; in *Hypericum* the humps are more pronounced and give five bundles of stamens (or three in the case of smaller flowers with rapidly falling phyllotaxis). In the Tiliaceae and Malvaceae the stamens also tend to be in *antipetalous* fascicles developed centrifugally on antipetalous humps of the young floral disc; in *Sparmannia* (Tiliaceae), however, they are antisepalous.

Fasciculation of this kind, resulting from prominent humping, or radial lobing, of the floral disc in its early stages seems very clearly to be connected with the diminution in size of the floral bud, and the humping, itself, seems to be caused both by the pressure of the perianth segments on the floral disc as they develop, and by their very close proximity with the incipient andrœcium. More detailed studies of floral development, by section and dissection, will doubtless explain the peculiar ridging of the young andrœcium. The basipetal elongation of the receptacular tissue of the humps, corresponding with the basipetal (or centrifugal) growth of the andrœcium, elevates each bundle of stamens on a common stalk, exactly as in the development of floral tubes.

Payer and many botanists after him have regarded fasciculate stamens as branched systems, or compound microsporophylls, derived from the repeated branching of the initial hump, as pinnae are produced on the compound leaf. When there is no visible stalk or axis to the hump, the staminal primordia which appear on it are supposed to have arisen by "congenital" branching in the solid mass of tissue. This is clearly a *reductio ad absurdum*. There are all transitions from the massive centrifugal andrœcium to the fasciculate state, e. g. Dilleniaceae, and one cannot conceive the evenly centrifugal and ring-like andrœcium of *Wormia* or *Bixa* either as compounded of congenital initials or as representing one amplexicaul sporophyll, not even from the point of view of the vascular bundles, as recently maintained (2, 9).[1] The centrifugal andrœcium is merely a reversal of the normal state, for the explanation of which we must consider what disturbance of the growth-processes can produce a reversal; fasciculation is an added complication which does not involve abstract morphology. That bilobed staminal primordia sometimes form on the floral disc does not indicate branching of a compound sporophyll but the manner of interference of unit-primordia on origin, exactly as bilobed and trilobed pores in Polyporaceae or spines in Hydnaceae indicate con-

[1] In the centrifugal flowers the initial androecial vascular bundles develop in spiral sequence after those of the perianth, thus indicating the normal acropetal organization of the interior of the floral apex; they then break up into a plexus immediately below the surface of the androecial disc, to supply its new departures.

genital fusion, from uneven spacing, of normally discrete primordia. Centrifugal enation in an asymmetric or confined space is far more likely to produce irregularities than the normal acropetal and centripetal process.

3. *Zonation.* In the Theaceae, the reduced andrœcium of *Visnea* develops five, initial, antisepalous stamens, then two more stamens beside

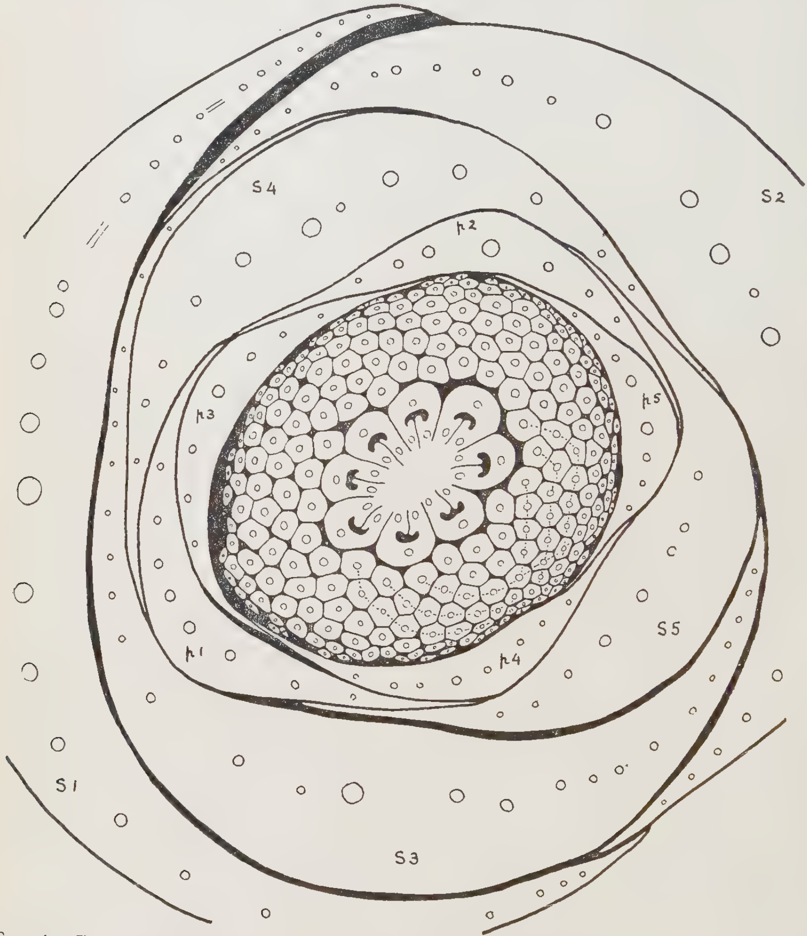

FIG. 4. *Wormia suffruticosa:* transverse section of a flower-bud about one-third grown (between stages *b* and *c* in *Fig. 3*), the stamens irregularly centrifugally whorled (20 + 20), the v. b. shown; × ca. 15.

each, first one on one side and then one on the other of each of the original five. Thus a single ring of 15 stamens is produced and it appears as the natural reduction of the massive, centrifugal andrœcium of *Thea* and *Gordonia* to the initial ring of 15; centrifugal growth of the andrœcial disc is so limited that only 10 slightly external stamens arise after the

first five and all appear inserted at the same level in the open flower. The andrœcia of *Portulaca*, *Philadelphus*, and *Citrus* seem to develop in the same way, but in *Citrus* there is prolonged tangential enlargement of the andrœcial disc which allows many more stamens to be intercalated in the same zone.

4. *Centrifugal obdiplostemony.* The andrœcium of *Visnea* is obdiplostemonous with an outer, though later, whorl of five pairs of antipetalous stamens. If one imagines the centrifugal growth of the andrœcium so

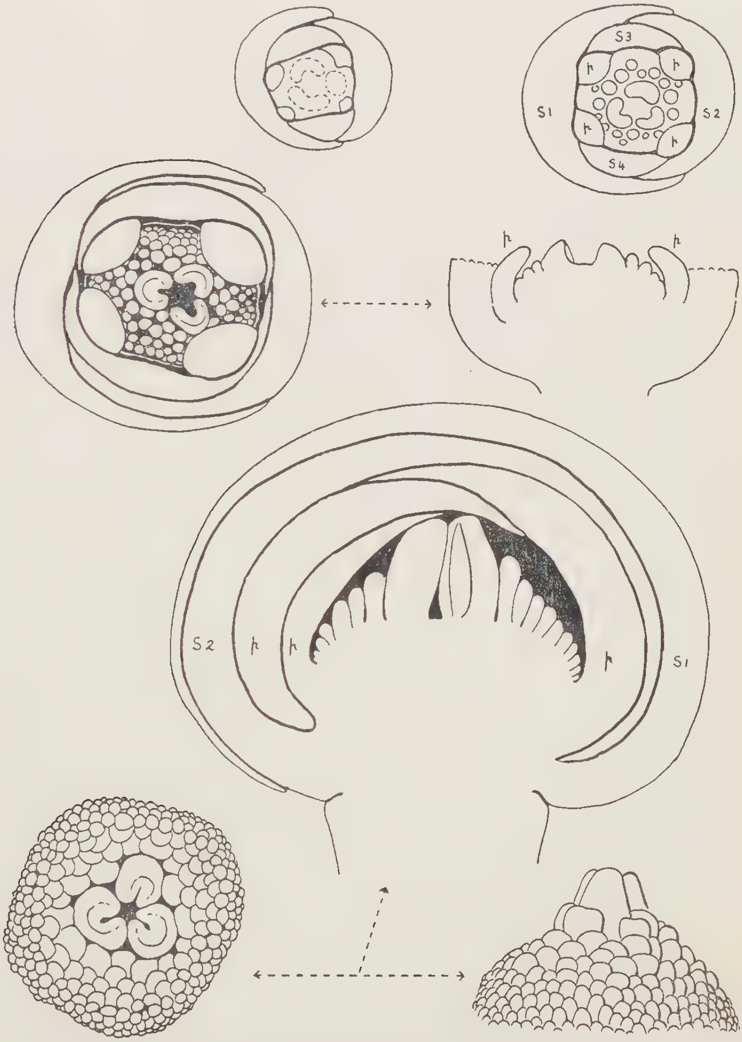

FIG. 5. *Tetracera Assa:* early stages in the development of the flower-bud (these buds with only 3 carpels); s = sepals (4), p = petals (4); × ca. 27.

limited that only one stamen can be inserted in each of the gaps between the initial five, then the 5 + 5 obdiplostemonous andrœcium will be formed, c. f. *Cistus* and *Helianthemum*. Such appears to have been the case in the Geraniaceae, for *Monsunia* has 15 stamens in two whorls, the outer (and later in development) consisting of five antipetalous pairs, while *Geranium* has only five stamens in the outer, and later, whorl. Similarly in the Zygophyllaceae, *Peganum* and *Nitraria* have 15 stamens as in *Monsunia*. Indeed, both families agree with the Rutaceae in showing traces of descent from the massive centrifugal andrœcium. The obdiplostemony of the Caryophyllaceae, Ericaceae, and Epacridaceae seems explicable in the same manner.

In the Capparidaceae, the reduction of the multistaminate state in *Capparis* has produced the 6-staminate condition of *Cleome*, in the slender little flowers of which the stamens develop centrifugally in 2 whorls, 2 + 4, to give the same tetradynamous arrangement as in the Cruciferae. Thus the cruciferous andrœcium appears to be another limiting state of the centrifugal gynoecium in the tetramerous flower.

According to Eichler, this was the interpretation of obdiplostemony given by Chatin, Pax, and Hofmeister; he affirms that in obdiplostemonous flowers the antipetalous stamens develop after the antisepalous (3, p. 336). It is noteworthy, as corroborative, that in monocotyledons staminal development is always centripetal and obdiplostemony seems not to occur (5, p. 297). In centrifugal obdiplostemony there is no interruption in the alternating whorls of the flower but a reversal in the direction of development of new stamens after the first whorl, and this reversal, in the limiting case of two whorls of n + n or n + 2n members, gives a false appearance in the mature flower. Nevertheless, in the Tiliaceae, Malvaceae, and Hypericaceae there is a form of obdiplostemony which does interrupt the sequence of alternating floral whorls, for the initial andrœcial humps in the floral bud are *antipetalous* and the reduction of their centrifugal andrœcia to two whorls would give apparent *diplostemony*. It is clear that our macroscopic interpretations of andrœcia will remain confused or uncertain until there is much more precise knowledge of the developmental sequence of the stamens and of the spacing factors in the floral bud.

PHYLETIC VALUE

The systematic importance of the centrifugal andrœcium is shown by the two instances of *Paeonia* and *Saurauja*.

Paeonia is usually placed in the Ranunculaceae, where its persistent sepals and distinct, if rudimentary, aril are anomalous. In 1908, Worsdell wrote (10):—

> "From a consideration of the character of the vascular anatomy alone I am sure that no one would ever dream of classing *Paeonia* with the *Ranunculaceae;* on the other hand, a very fair case could be made out for classing the genus with the *Magnoliaceae*."

Worsdell proposed the family Paeoniaceae as a link between the Ranunculaceae, Magnoliaceae, and Calycanthaceae. Yet, the two anomalies of persistent sepals and aril still remain, and the comparison with the Magnoliaceae introduces three or more anomalies in the pinnate leaves, the acyclic calyx and corolla, and the flat receptacle of *Paeonia*.

In 1932, Schöffel discovered that the andrœcium of *Paeonia*, consisting of 200 or more stamens, developed centrifugally on a slightly raised staminal disc (evidently as in *Wormia*), and that this feature was unique among the Ranunculaceae (6).

If, now, we follow this clue and compare *Paeonia* with the Dilleniaceae,

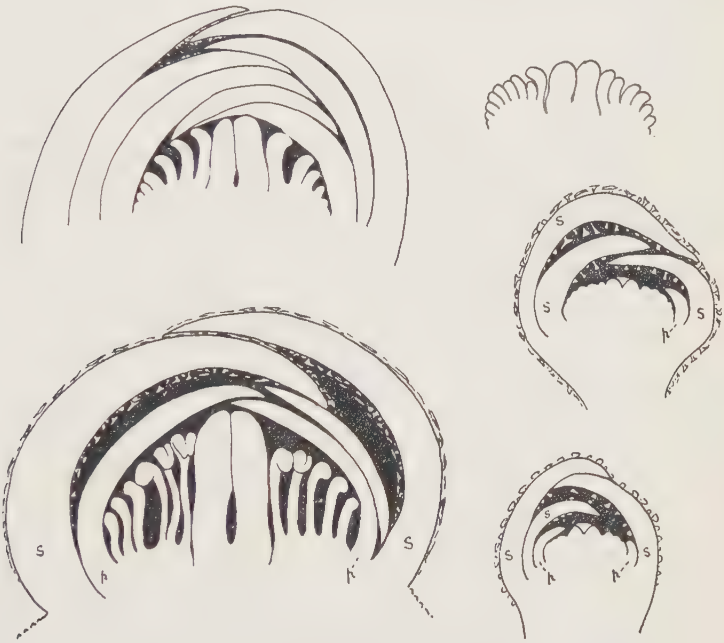

FIG. 6. *Bixa Orellana*: early stages in the development of the flower-bud; s = sepals, p = petals; × ca. 27.

we find that the vascular character emphasized by Worsdell, the persistent sepals, the aril, the hard testa, the woody tendency and, even, the pinnate, exstipulate leaves are as much dilleniaceous as the centrifugal andrœcium. Dilleniaceous leaves are typically simple, but the large, acropetally developing, toothed leaves of *Dillenia* give every appearance of a webbed pinnate leaf, and in the dwarf shrubs, or woody herbs, of *Acrotrema* there are species with doubly or simply pinnatifid leaves and simple leaves. Indeed, there are no obvious features to separate the Paeoniaceae from the Dilleniaceae, particularly if *Actinidia* is included among them. *Paeonia,* thus, appears naturally as a temperate derivative of the Indo-Malaysian

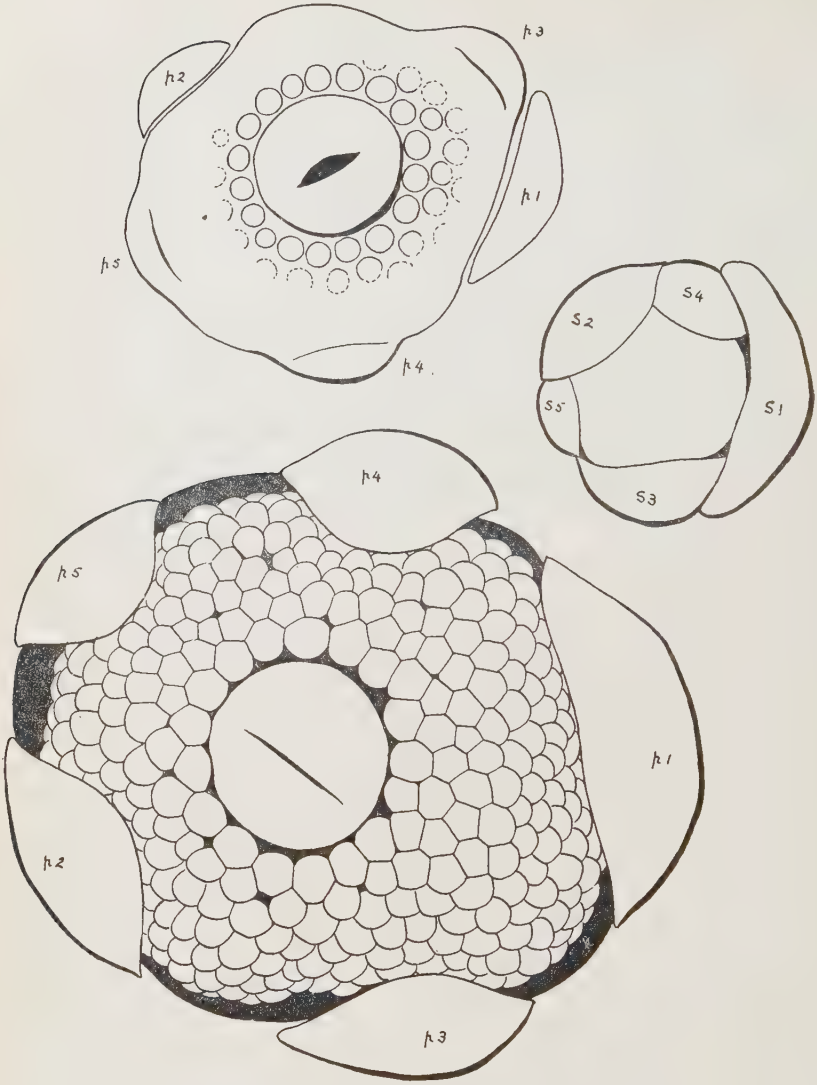

FIG. 7. *Bixa Orellana*: early stages in the development of the flower-bud in surface-view, × ca. 45.

Dilleniaceae closely comparable with *Actinidia*. It is not at all odd that they should be typically oriental, for the great land-mass of southern China has been the only part of the world where the tropical flora has been able for ages to invade over a vast front the north temperate region. It is worth noting, too, that another anomalous genus, *Crossosoma*, which has

been put in the Dilleniaceae, was classed by Baillon with *Paeonia* (1, p. 66).

Saurauja is another problematic genus which has been placed in the Dilleniaceae, the Theaceae, and, with *Actinidia,* in the Actinidiaceae. Brown has shown that its andrœcium is centrifugal, exactly as in the Dilleniaceae and Theaceae. This agreement clinches the close affinity between the two families; and, again, the Theaceae appear naturally as an oriental and temperate off-shoot of the older, Indo-Malaysian Dilleniaceae.

A third instance, far less certain, through lack of knowledge, may be found in the Parietales as a whole. The series appears to be a very vague group of diverse families without any character in common, not even the placentation. It is a natural group by "concatenation." Yet, so far as known, the andrœcium is centrifugal in six families—Hypericaceae, Cistaceae, Dilleniaceae, Theaceae, Bixaceae, and Loasaceae; it may well be centrifugal also in the Ochnaceae, Caryocaraceae, Guttiferae, and Flacourtiaceae. It is centrifugal in the allied Opuntiales.

From these considerations I am compelled to regard the centrifugal andrœcium as a most important systematic character which defines, as a natural phylum, a large number of dicotyledonous families at present confused with other series of families possessing the centripetal andrœcium. On the one hand there are the primary ranalian, rosalian, myrtalian series and, on the other hand, there is the centrifugal series derivative from one or other of the primary series, or their ancestors. It is likely that, beside the Parietales and Opuntiales, most of the Geraniales, Malvales, Centrospermae, and Ericales belong to the centrifugal series.

Dogmatic and biased as this may seem at first sight, yet a clear standpoint is to be preferred when a new idea emerges. Morphologically I would expect so profound a disturbance in floral development as the reversal of the andrœcium to be highly peculiar and, therefore, phyletic. On the other hand, particularly in flowering plants, we know that homoplasy is general, that such floral features as sympetaly, synandry, syncarpy, epigyny, and so on, have arisen independently in many different series, for which reason we might consider the centrifugal andrœcium as merely another instance of this confusing phenomenon. Yet, one must remark that, whereas all such homoplastic features occur in many different dicotyledonous *and* monocotyledonous series, the centrifugal andrœcium does not occur among the monocotyledons, and among the dicotyledons it is centered around the Parietales. Therefore, I think one must regard as anomalous the association of the centrifugal Capparidaceae *cum* Cruciferae with the centripetal Papaveraceae in the Rhoeadales and that of the centrifugal Lecythidaceae with the centripetal Myrtaceae and Lythraceae in the Myrtales. One must ask whether they have not been as mistakenly classified as *Paeonia* with the Ranunculaceae. And the position of all obdiplostemonous families must come under review.

NOTATION

The symbols A ∞ and An + n . . . must be resolved into

$A\ \overrightarrow{\infty}$ and $A\ \overleftarrow{\infty}$ for centripetal and centrifugal stamens, respectively; and

$A\ \overrightarrow{n} + n \ldots$ and $A \ldots n + \overleftarrow{n}$.

Thus, a major difference between the Ranunculaceae and the Dilleniaceae can now be shown in their floral formulae.

For the Lauraceae, we may write $A\ \overrightarrow{3} + 3 + 3 + 3$, but for *Capparis* $A \ldots 32 + 16 + 8 + 4 + \overleftarrow{4}$.

Monsunia becomes $A\ 10 + \overleftarrow{5}$, and *Geranium* $A\ 5 + \overleftarrow{5}$, while *Brownea* may be $A\ \overrightarrow{5} + 5 + 5$ and *Caesalpinia* $A\ \overrightarrow{5} + 5$.

In the case of the fasciculate stamens, we may write $An(\overleftarrow{\infty})$, as in *Hypericum* $A\ 5(\overrightarrow{\infty})$.

For zonate stamens, the notation is more difficult, but it may suffice to write $A\ \overleftrightarrow{n}$ or $A\ n + \overleftrightarrow{m}$, where n is the number of initials and m the number of stamens intercalated between them. The symbol $A\ \overleftrightarrow{\infty}$ would imply amphipetal development of the androecium, which is not known.

Obdiplostemony appears to be represented better by

$Kn\ Cn\ A\ n + \overleftarrow{n}\ Gn$

than by the usual formula

$Kn\ Cn\ A\ \overrightarrow{n} + n\ Gn$.

SUMMARY

1. A list of 13 families of dicotyledons is given in which the stamens develop centrifugally. The mechanism is explained in detail for *Wormia, Tetracera,* and *Bixa.*

2. The centrifugal andrœcium appears to be a feature of considerable systematic importance which indicates a common origin for the families in which it occurs. Thus the Paeoniaceae, with centrifugal andrœcium, are referred to the Dilleniaceae rather than to the Ranales.

3. The primitively massive, centrifugal andrœcium must have been derived from the usual centripetal state. Reduction-specialization, leading to fasciculate, zonate, and diplostemonous andrœcia, seems to have occurred in both kinds of flower, resulting in a confusion in classification which takes no account of manner of development. Particularly is this so in obdiplostemonous families, e. g. Geraniales, Centrospermae, and Cruciferae, which seem referable to the centrifugal series.

4. There is no evidence that centrifugal fasciculate stamens (Hypericaceae, Tiliaceae, Malvaceae, Dilleniaceae) are branched sporophylls.

5. More critical notation for the andrœcium in the floral formula is suggested.

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NEW CYATHEACEAE FROM COLOMBIA

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With one plate

RECENT exploration in Colombia gives indication of a far richer fern flora than has previously been known from that country. This is true especially of the tree-ferns (Cyatheaceae), in which perhaps not more than half the specimens of several large collections can be identified with reasonable certainty. To me the more interesting members of the family are those species — mostly small plants — with pinnate-pinnatifid fronds, in habit and general appearance most resembling various species of *Dryopteris* (Polypodiaceae), and I have previously published descriptions of nearly a dozen from tropical America as new. Of the four additional species here described three are of the sort mentioned, with pinnate-pinnatifid fronds. The fourth, *Alsophila mollicula,* is quite unlike these in having the blades fully bipinnate, the secondary pinnae deeply pinnatifid; it is not approached by any of the diminutive tropical American species thus far known.

Cyathea rupestris sp. nov.

Caudex erectus, fortasse 10–12 cm. longus (pars 6 cm. longa adest), 1.5–2 cm. diam., apice et inter cicatrices rotundas ca. 5 mm. diam. appresso-paleaceus, basi crasse radicosus; paleae subdeltoideae, 2–3 mm. longae, 1–1.7 mm. latae, apice obtusae vel subacutae, basi subcordata affixae, parte media castaneae, densae nitidaeque, marginibus latis cinnamomeis teneris laxe et varie fimbriatis. Folia plura, patentia, 40 cm. longa; stipites ca. 5 cm. longi, 3–4 mm. diam., atropurpurei, inermes, basi appresso-paleacei; laminae lanceolatae, ca. 35 cm. longae, 10–11 cm. latae, acuminatae, pinnato-pinnatifidae, rhachi atropurpurea, infra nuda et glabrescente, supra crebre brunneo-hispida et paleis linearibus laxis pallidis tenuibus instructa; pinnae majores ca. 20-jugae, sessiles, inferiores oppositae et plus minusve deflexae, mediales suboppositae, patentes, anguste oblongae, acuminatae, 5–6 cm. longae, 11–14 mm. latae, profunde pinnatifidae (pleraeque basi pinnatisectae), subcoriaceae, supra costa hispida excepta glabrae, infra costis et costulis pilis brunneis rigidis paucis praeditae; segmenta ca. 12-juga, oblonga, subfalcata, 5–7 mm. longa, medio 3–3.5 mm. lata, obtusa vel antice subacuta, marginibus subintegris leviter revolutis, plerumque anguste conjuncta, ala costali utroque latere ca. 1 mm. lata; venae 7- vel 8-jugae, plerumque furcatae, obliquae, infra modice elevatae, cum parenchymate glabrae; sori 3-jugi, basales, contigui, indusiis hemisphaericis, brunnescentibus, membranaceis; sporangia numerosa; paraphyses ut videtur nullae.

TYPE in the U. S. National Herbarium, No. 1,852,149, collected along the Río Margua, between Junín and Córdoba, region of Sarare, in the Cordillera Oriental, Departmento Norte de Santander, at 920 to 1240 meters elevation, among rocks, November 22, 1941, by J. Cuatrecasas (No. *13396*).

In general appearance only *Cyathea rupestris* somewhat recalls *C. Nockii* of Jamaica. That species differs markedly, however, in its heavier caudex and much larger fronds, these fully bipinnate, the vascular parts pale and conspicuously paleaceous throughout.

Hemitelia decorata sp. nov. PLATE I.

Caudex erectus, usque ad 3 m. altus, ca. 3 cm. diam., inermis, inter cicatrices remotas fusco-vernicosus, dense imbricato-paleaceus, paleis lanceolatis, acuminatis, 7–9 mm. longis, 1.5–2 mm. latis, fusco-castaneis, opacis, marginibus anguste ochroleucis subintegris, paleis apice ipso majoribus, usque ad 14 mm. longis, marginibus pallidis multo latioribus. Folia 6–8, rigide adscendentia, 100–110 cm. longa; stipites 10–20 cm. longi, 5–7 mm. diam., ochracei, verrucosi, crebre hispidi (pilis pallide ferrugineis 6–9 mm. longis), ubique dense paleacei, paleis basalibus anguste triangularibus, usque ad 15 mm. longis, medio castaneis, marginibus pallidis latis, paleis sursum laminam versus numerosis, conspicuis, oblongo-lanceolatis, acutis, usque ad 2 cm. longis et 6 mm. latis, flavo-brunneis, lucidis, late imbricatis, subintegris, persistentibus; laminae anguste lineari-oblanceolatae, abrupte acuminatae, 85–100 cm. longae, 24–30 cm. latae, pinnato-pinnatifidae, rhachi ubique dense hispida sed basi excepta paleis carente; pinnae 35–40-jugae, proximae, patentes (jugae inferiores deflexae), ligulatae, acute vel abrupte acuminatae, 11–15 cm. longae, 2.2–3.2 cm. latae, pinnatifidae, herbaceae, costis supra hirsutis, infra longe hispidis; segmenta 15–20-juga, patentia, proxima, late oblonga, rotundato-obtusa, 9–14 mm. longa, 5–6 mm. lata, leviter (raro profunde) crenata, costulis venisque utrinque laxe hispidis vel hirsutis, parenchymate glabro; venae 6- vel 7(8)-jugae, medio furcatae; sori 4–6-jugi, mediales, rotundi, ca. 1.3 mm. diam.; indusia ampla, profunde saccata, integra, demum 2- vel 3-lobata, brunnescentia; receptaculum magnum, globosum; paraphyses nullae.

TYPE in the U. S. National Herbarium, Nos. 1,852,571–573, collected in forest along the Río Yurumangui, Department of El Valle, altitude 5 to 50 meters, January 28 to February 10, 1944, by J. Cuatrecasas (No. *15737*).

The following additional specimens, all in the National Herbarium, have been studied: Córdoba, Dept. El Valle, alt. 80–100 m., in forest, *Killip 5257*; Río Cajambre, Dept. El Valle, alt. 5–80 m., in forest, *Cuatrecasas 17429*; Agua Clara, along highway from Buenaventura to Cali, Dept. El Valle, alt. 100 m., in dense forest, *Killip & Cuatrecasas 38914*; dense forest south of Río Condoto, between Quebrada Guarapo and Mandinga, Intendencia del Chocó, alt. 120–180 m., *Killip 35192*; ridge along Yeracüi Valley, Corcovada Region, upper San Juan, Intendencia del Chocó, alt. 200–275 m., *Killip 35334*.

Hemitelia decorata is apparently not uncommon in the Pacific lowland region of Colombia, having first been brought out by Killip in 1922. The excellent series of specimens cited shows remarkably little variation, although the plants are of various ages, with stems ranging from 30 centimeters to 3 meters tall. The widely imbricate, persistent covering of large, fawn-colored scales upon the stipes is a notable feature, suggesting the desirability of introducing this beautiful plant into cultivation.

Hemitelia pumila sp. nov.

Rhizoma adscendens, 5 cm. longum, 1.5 cm. diam., parte apicali copiose imbricato-paleaceum, deorsum radicosum; paleae lineari-attenuatae, apice

subfiliformes, 5–7 mm. longae, 0.5–0.7 mm. latae, albidulae, concolores, tenerae, subintegrae. Folia plura, adscendentia, ca. 50 cm. longa; stipites 15–18 cm. longi, 1–1.5 mm. diam., sulcati, inermes, brunneo-olivacei, glabri, paleis patentibus albidulis linearibus laxis tenuiter praediti; laminae oblongae, acuminatae, ca. 35 cm. longae, 12–14 cm. latae, pinnato-pinnatifidae, rhachi supra hispidula, subtus glabra; pinnae majores ca. 10-jugae, subremotae, patentes, lineari-oblongae, acutae, 6–7.5 cm. longae, 1.5-2 cm. latae, conspicue petiolulatae (usque ad 7 mm.), grosse pinnatifidae vel inferiores basi superiore pinnatisectae, subtus omnino glabrae, supra costis tenuiter hirtellis; segmenta membranaceo-herbacea, 9- vel 10-juga, pleraque late oblonga, apice rotundata, maxima 6–8 mm. longa, sinu acuto 5–6 mm. lata, et ala costali utroque latere 2–3 mm. lata conjuncta, solum segmentum basale anticum pinnarum inferiorum nonnullarum sessile vel subsessile, ovale, marginibus undulatis vel leviter dentato-crenatis; venae 6-jugae, apicales exceptae ad vel ultra medium furcatae, obliquae, tenues; sori 1–3-jugi, inter se remoti, mediales vel supramediales, plerumque furca venarum siti; indusium parvum, brunnescens, obdeltoideum, modice concavum, subintegrum; receptaculum parvum, globosum, paraphysibus numerosissimis elongatis diffuse et irregulariter ramosis onustum.

TYPE in the U. S. National Herbarium, Nos. 1,875,038–9, a unicate collected on the Cerro del Castillo, Upper Apaporis Basin, near confluence of the Ajuju and Macaya, Territorio del Caquetá, at about 540 meters altitude, in wet shady forest, on sandstone, July 27, 1943, by R. E. Schultes (No. *5664*).

Although the present species is almost certainly distinct, its proper generic reference is doubtful, if one chooses to maintain the traditional genera of Cyatheae. It might, in fact, almost as well be placed in *Alsophila* as in *Hemitelia,* since the indusium is reduced to a triangular, slightly concave structure scarcely typical of *Hemitelia* and, except for its greater breadth, not very different from the minute vestigial scale that may be observed in several species of *Alsophila.* So far as I know, it is without any very near relatives.

Alsophila mollicula sp. nov.

Rhizoma deest. Folia plura, laxe adscendentia, 55 cm. longa; stipites 15 cm. longi, 2–3 mm. diam., spinis ad 1.5 mm. longis castaneis cylindricis gracilibus instructi, basi comoso-paleacei, paleis filiformibus, leviter flexuosis, 10–15 mm. longis, 0.2–0.3 mm. latis, basi castanea minuta excepta pallide ferrugineis, sursum copiose hispidi, pilis plerumque 5–6 mm. longis, pallide ferrugineis; laminae ovatae, acuminatae, 40 cm. longae, 25 cm. latae, bipinnato-pinnatifidae, rhachi sicut stipite longe hispida, paleis nullis; pinnae ca. 14-jugae, patentes, inferiores (2 jugae) suboppositae, remotae, breviter petiolulatae, alterae alternae, plerumque triangulari-oblongae, acuminato-caudatae, basi valde acroscopicae, maximae 13 cm. longae, basi inaequilaterali 2.5–3.5 cm. latae, tenuiter herbaceae, plane pinnatae; pinnulae proximae, oblongae, apice rotundato-obtusae, basales superiores maximae, sessiles, 15–20 mm. longae, 6–8 mm. latae, pinnatifidae, lobis obtusis costulae latere utroque ala ca. 1 mm. lata conjunctis, costulis et venis utrinque abunde laxe hirsutis; venae 2- vel 3(4)-jugae, obliquae, tenerae, simplices vel infimae rarissime furcatae; sori 1- vel 2-jugi, pusilli, mediales, sporangiis paucis; receptaculum minutum; paraphyses simplices, tenues, moniliformes, griseae, sporangia saltem aequantes.

HEMITELIA DECORATA MAXON

TYPE in the U. S. National Herbarium, No. 1,804,961, collected between Santa Marta and Marsella, Territorio del Caquetá, August 4, 1926, by G. Woronov and S. Juzepczuk (No. *6415*). Two fronds of this number in the herbarium of the Komarov Botanical Institute of the U. S. S. R., Leningrad, are nearly identical with the type. The rhizome, unfortunately wanting, was presumably a slender erect caudex.

As mentioned above, the bipinnate-pinnatifid fronds of *A. mollicula* are wholly distinctive for so small a plant in this genus. In a general way the leaf dissection suggests several of the smaller species of *Dryopteris,* subgenus *Ctenitis,* particularly *D. nemorosa* (Willd.) C. Chr., of Puerto Rico and Hispaniola.

EXPLANATION OF THE PLATE

Hemitelia decorata Maxon: photograph of one sheet of the type specimen, about two-fifths natural size.

UNITED STATES NATIONAL MUSEUM,
WASHINGTON.

PRELIMINARY REVISION OF THE GENUS LONICERA IN MALAYSIA

C. G. G. J. VAN STEENIS

With two text-figures

IN MY yet unpublished "Javanese Mountain Plants in Colours" I recognize two indigenous species of *Lonicera*, as did Blume in his "Bijdragen," p. 653, 1825. Topotypes are abundant in the Buitenzorg Herbarium. The question arose which were the appropriate names for the Javanese species, as the naming of the herbarium material was in some disorder. The latest suggestion was (in herb.) that of C. A. Backer and W. M. Docters van Leeuwen, who assumed that *L. Loureiri* represented only an extreme "alpine" form of *L. javanica*; hence, they recognized only one variable species in Java. Since I could not agree to this, I made a study of all Malaysian *Lonicerae* present in our herbarium. As I have not seen types of several extra-Javanese "species," my conclusions are provisional.

The genus is by no means a difficult one but, on the other hand, there is a rather large variability in characters supposed to be important for specific distinction, extreme forms from isolated populations along the borders of the generic area being described as separate species. In dried material dimensions are often misleading; immature buds open slightly during drying and appear to be mature. *Lonicera sumatrana*, for example, described by Miquel, was based on bud material and thus misplaced in Rehder's monograph. For this reason it was not identified with *L. leiantha* Kurz and later was redescribed by Merrill as *L. jasminifolia*.

I am of the impression that in *Lonicera* too much stress has been laid on density of pubescence. To me the colour of the indumentum is more important. Of the four Javanese species recognized I am familiar with three in the living state, and I feel that it is of importance to know whether the upper lip is straight or whether both lips are recurved, the latter a character which probably goes parallel with the texture of the corolla. This difference is very striking in the Javanese species, but is not always readily distinguishable in herbarium material.

In the Javanese species, of which I have studied abundant material, the shape of the calyx-lobes, bracts, and bracteoles and their pubescence are rather variable, as are the shape and dimensions of the leaves and their pubescence. It seems urgent to me to obtain a clear idea of characters fit for specific distinction in the section NINTOOA and both of its subsections. The reduction of 13 names to only four species suggests a further reduction in the section.

I wish to draw attention to the possibility of polygamy as studied by Docters van Leeuwen, another testimony that geographical and ecological studies of plants cannot be carried on without an exact taxonomic knowledge. Docters van Leeuwen described *L. javanica* in his work on the "Biology of Plants and Animals Occurring in the Higher Parts of Mount Pangrango-Gedeh in West Java" (Verh. Kon. Akad. Wet. A'dam sect. II, 31: 235–239. 1933) and remarked that according to him only one species occurred in Java. His material belongs to *L. acuminata* (= *L. Loureiri*), as true *L. javanica* does not occur on the summit of Mt. Pangrango, where the altitude ranges from 2400 to over 3000 m. *Figure 60* in his study suggests *L. javanica*, while *fig. 61* is doubtless

Fig. 1. Geographical distribution of the genus *Lonicera* in Malaysia, showing the two migrational routes.

L. acuminata. The first he calls the "bisexual" form. However, the dimensions of the flower, the two recurved lips, and the protruding anthers and style suggest identity with *L. javanica*.

In the "female" form which, according to his description, is certainly *L. acuminata* (= *L. Loureiri*), he describes the erect upper lip as forming a hood which covers most of the stamens and states: "the anthers which remain closed do not contain pollen." Yet, of so-called galled inflorescences with small flowers which hardly open he remarks: "the stamens which still may produce pollen remain hidden." Whether female forms of *L. acuminata* with sterile stamens occur I do not know; this must be further studied in the field.

All Malaysian species have the normal colour of the flower, i. e. creamy in buds and freshly opened flowers, yellow or orange in old flowers. Each is reported to be fragrant. Sometimes, the twigs of *Lonicera* are claimed to be used as a substitute for binding purposes (probably in emergency cases).

When dealing with Malaysian mountain plants which have originated on the southeastern Asiatic continent, one always must be extremely cautious in separating them from the Asiatic alliance and in classifying them as distinct species which are endemic in Malaysia. In addition to the great probability that the isolation has induced the Malaysian representatives to gain subspecific or racial value, the study of Indian and Malaysian species by various authors in different herbaria must be carefully considered; often these authors have limited themselves to the material in their country in order to avoid enlarging their study for which they needed material from other herbaria. Monographers sometimes follow the "current opinion" of earlier works and of botanists who confine themselves to administration rather than critical unbiased study. And local botanists often consider it outside their realm of work to combine their species with others of neighbouring countries, though they often hint at the possibility. This mutual disinclination to join forces leaves the identity and status of the plants often unsolved. Sumatran, Javanese, and Malay Peninsular mountain plants cannot be studied without consulting the southeastern Asiatic species. *Lonicera sumatrana,* in my opinion, occurs in Burma and Siam (under the name *L. leiantha*), and I expect *L. pulcherrima* and *L. javanica* also occur (under other names) on the Asiatic continent: *L. acuminata*, which I accept in the Hookerian sense, has the widest range.

For the sake of convenience I have made a key for the two cultivated and the four wild Malaysian species and I have added remarks under the latter. To facilitate naming duplicates in other herbaria I have mentioned the collector's numbers under each of them.

My provisional enumeration of the Malaysian species, in Bull. Jard. Bot. Buitenz. III, 13: 179. 1934, is herewith corrected.

KEY TO THE WILD AND CULTIVATED SPECIES OF LONICERA IN MALAYSIA

1. Each cyme of 2 flowers sustained by 4 bracteoles and 2 *leafy* bracts; filament and style glabrous; cultivated. .... 1. *L. japonica* Thunb.
1. Bracts not leafy .... 2.
2. Ovary hairy all over; cultivated, but rather rare (Medan, Singapore) .... 2. *L. confusa* DC.
2. Ovary glabrous (except the apex in *L. pulcherrima*). .... 3.
3. Plant entirely glabrous (except few hairs on stamens and style and small negligible ciliae on the edge of the calyx and the bracts); inflorescence loose, few-flowered; flowers 4–5 cm. long, the 2-flowered peduncles slender; nerves few, slightly prominent, the reticulations indistinct or hardly visible. ....3. *L. sumatrana* Miq.
3. Hairy, at least the petiole; nerves and reticulations distinct, prominent. .... 4.
4. *Corolla short but relatively thick, 13–20 mm. long* (s. s.), the *tube 1.5–3 mm. diam.*, the *upper lip* straight in opened flowers, the lower lip recurved; corolla of thick texture, not with glandular hairs; inflorescence *dense*, *short*, mostly not

exceeding the upper foliage; thickened part of the bud about as long as the tube; stamens, at least 3 of them, included under the upper lip; pubescence rather rough, *yellow*, its density variable; leaves *mostly rugose*, sometimes subbullate, the midrib *always* hairy on the upper surface nearly to the apex, the leaves not glaucous beneath. ....4. *L. acuminata* Wall.

4. *Corolla 18–50 mm. long, the tube slender, 1–2 mm. diam.*, when mature *both lips recurved*; texture of the corolla thin; inflorescence *not contracted*, often foliaged, paniculate, with glandular hairs, mostly exceeding the leaves; pubescence not rough, often not yellow; midrib often glabrous above; leaves *glaucous* beneath. ...... 5.

5. Style slightly hairy; flowers long, mostly in dense rich-flowered *Ixora*-like, globose terminal inflorescences exceeding the leaves, in subumbelliform clusters at the ends of the upper axillary stalks; peduncles contracted with a conspicuous yellow tomentum which continues on the internodes of the twigs and is interspersed by dot-like, red glands; twigs not wiry and not glossy red-brown, but stiff; pubescence of the calyx-teeth often descending on the upper portion of the ovary. ....5. *L. pulcherrima* Ridl.

5. Style glabrous; flowers medium-sized, in less rich-flowered inflorescences, the stalks mostly with a grey tomentum, the red sessile glands absent; twigs ± wiry, soon conspicuously shiny red-brown, slender; ovary glabrous. ....6. *L. javanica* DC.

3. **Lonicera sumatrana** Miq. (*L. leiantha* Kurz, *L. jasminifolia* Merr.).

By its glabrousness, subtriplinervous leaves without distinct reticulations, and poor-flowered lax inflorescences this species is clearly distinct from all other Malaysian representatives. The ovary also offers distinction: it is constricted at the apex, with the part of the calyx which is free from the ovary splitting halfway down so as to form a short tube, which, in turn, is much shorter than the ovary. The bracts are about half as long as the ovary, and the bracteoles are still smaller. In the other Malaysian species the free part of the calyx consists of five separate triangular to subulate lobes.

SUMATRA: *Yates 2534; Teysmann 1039 HB; Lörzing 6602; Kleinhoonte 558;* all from the Toba-region and Sumatra Westcoast; and *Ajoeb* (exp. *Jacobson*) *181* from Rimbo Pangadang in the Res. Benkoelen.

The species occurs in Burma, Siam, North and Central Sumatra, between 1000 and 1250 metres altitude. Lörzing mentions the flower as white, later yellow; Kleinhoonte claims the colour to be "rosa-like beige." It is a submontane plant occurring in forest borders.

Rehder placed this species incorrectly in the subsection BREVIFLORAE because of the fact that Miquel described the flowers from the immature bud state.

I have seen type specimens of *L. sumatrana* (*Teysmann 1039 HB* from Alahan Pandjang, Sumatra Westcoast) and *L. jasminifolia* (*Yates 2534* from Tapanoeli). These are quite identical. Of *L. leiantha* I have seen only the description. With Rehder's key one determines directly to *L. leiantha*. Kurz' description is also wholly fit for Sumatran plants. Because of these facts, I feel that all these names represent a single species, at which Merrill has already hinted.

4. **Lonicera acuminata** Wall. ex Roxb. (*Caprifolium Loureiri* Bl., *Lonicera Loureiri* DC., *L. oxylepis* Miq., *L. Leschenaultii* Miq. non Wall., *L. philippinensis* Merr., *L. Rehderi* Merr., *L. Giraldii* Rehder).

Ultimate twigs thick, *1.5–3 mm. diam.*, ruddy, *not* conspicuously shining brown, the inflorescences, leaves, etc., with *yellow rather hirsute* hairs, or glabrate. Petiole *hairy*. Leaves mostly *rugose*, sometimes subbullate, the lower surface *not glaucous*, the hairs on the lower surface scattered or nearly absent, the glandular-tipped hairs *absent*, the margin of the blade often *recurved*, sometimes entirely flat, the upper side of the blade often rather glabrous, but *the midrib pubescent nearly to the apex*. Inflorescences terminal and lateral in only few (2) axils, moderately or very *dense* as the upper internodes are short, *never* a loose panicle; inflorescence *seldom exceeding the foliage*, more or less embedded in it (also in fruit). Calyx-lobes ciliate, with few stiff hairs on the back. Buds rather *short and thick*, the *enlarged upper portion about as long as the lower part*, which is relatively thick, *2–3 mm. diam*. Opened flowers about 13–20 mm. long (s. s.). Corolla-lobes 3–4 mm. broad, the *upper lip straight*, the lower lip *recurved*. Style about as long as the corolla. Stamens about *as long as or shorter than the (expanded) corolla*, pubescent or glabrous. Anthers large, *2.5–5 × 0.5–1 mm*. Style pubescent or glabrous.

SUMATRA: *Bünnemeijer 891, 9453, 9811.*

JAVA: *Backer 478, 3293, 3301, 5054, 5081, 9727, 13530, 22345; Bakhuizen van den Brink 35; Bruggeman 79; Docters van Leeuwen 123, 1159, 2516, 8207, 8352, 8353, 8739, 8942, 12262, 21709; Hallier f. 478, 480; Koorders 15632, 25975, 32215, 32217, 37359, 38271, 40367, 40920, 43538; van Slooten 2627; van Steenis 1990, 4056, 4870, 7428, 10917.*

BALI: *Sarip (R. Maier) 376.*

PHILIPPINES: Bureau of Science *31886, 40232 (L. philippinensis).*

The species is interpreted in the current sense of Blume (we possess a number of topotypes), Hasskarl, Hooker, Rehder, and Koorders. There is no question about its identity. Backer (in herb. Bogoriensis) expresses as his opinion that *L. Loureiri* and *L. javanica* represent the same species. Blume already mentioned the different altitude at which both species occur in Java, *L. Loureiri* thriving especially on summits and *L. javanica* in forests. If we study the altitudinal zone for all specimens together we have 1000–3300 m. If we separate *L. Loureiri* and *L. javanica* we find *L. Loureiri* at 1600–3300 m. and *L. javanica* at 1000–2000 m. This would indicate that the altitudinal ranges overlap. However, the altitudinal range is more intricate than it appears if we arrange separately the specimens found on each mountain. Then we obtain the distribution shown in FIG. 2.

From this table it appears that the altitudinal ranges do not overlap. Only on Mts. Patoeha and Gedeh in West Java do the ranges touch one another. No intermediate specimens have been found; both species show a "healthy" variability. However, it is not actually known whether they can grow together at the same location without intermingling. They might represent altitudinal exotypes (altecotypes versus planecotypes), the more so as both species occur in Java and Bali and "accompany" one another. The chance is small, as the differential characters are numerous and distinct. I shall study this later in the field.

As to the altitudinal occurrence, it is to be noticed that the general aspect of "Massenerhebung" is also here represented. If we examine FIG. 2, it appears that *L. acuminata* occurs between 1600 and 3300 m. but

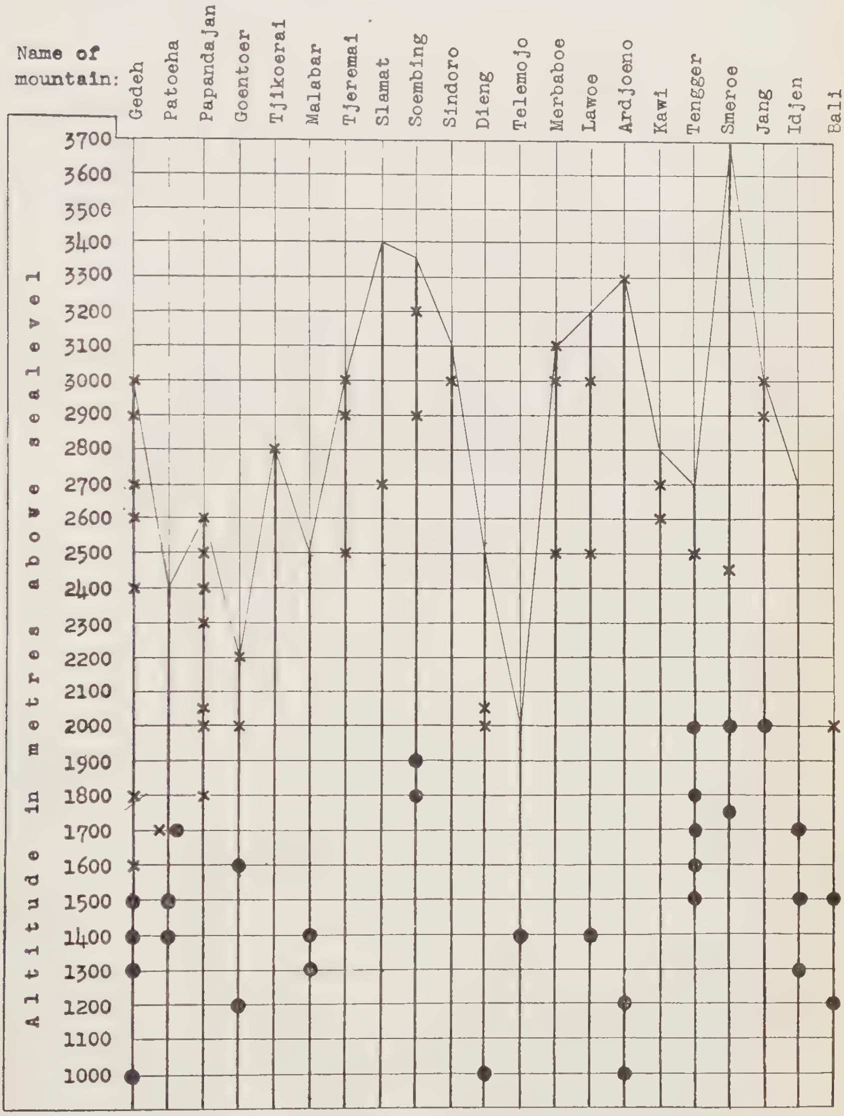

FIG. 2. Occurrence of *Lonicera acuminata* (crosses) and *L. javanica* (solid spots) in Java and Bali. The names of the mountains have been arranged, from left to right, in a west-to-east direction. The crosses and spots represent the altitude of the localities, while the thickened lines represent the altitudes of the summits of the various mountains.

only on mountains which themselves reach at least 2200 m. alt.; on these mountains it descends as low as 1600 m. In E. Java the lower limit is situated higher (at about 2500 m.), and *L. javanica* also reaches its highest stations there at about 2000 m., whereas in W. Java it is collected only up to 1700 m. On most mountains scarcely attaining 2200 m., such as Mts. Boerangrang, Tangkoeban Prahoe, Wajang, Windoe, Boekit Toenggoel, Galoenggoeng, Telagabodas, Oengaran, and Telemojo, *L. acuminata* has not been found.

On account of the occurrence of *L. Loureiri* in Sumatra, SE. Asia, and the Philippines, one would suspect *L. javanica* also to occur throughout that range, but as far as our material goes *L. javanica* has not yet been collected in Sumatra. On the other hand I suspect that *L. javanica* represents a race or subspecies of some SE. Asiatic species, in a widened specific concept, a concept which I think is badly needed in *Lonicera*.

My conclusion is that the status and distribution of *L. Loureiri* are sound but those of *L. javanica* are less satisfactory.

In some specimens I have found 3-verticillate leaves. The flowers occur sometimes in threes instead of twos. It is peculiar that the hairs on the corolla in *L. Loureiri* and *L. javanica* are directed toward the base of the corolla.

Lonicera Rehderi Merr. (1905) is described from the Philippines. On account of the fact that it is described with hairy midrib, the flowers about 2 cm. long, setosely pilose, in a crowded terminal inflorescence, the corolla-limb as long as the tube, I believe it to represent *L. acuminata*. As such it was identified at first according to Merrill's publication. Merrill says that, according to Rehder, *L. Rehderi* should differ from both *L. Loureiri* and *L. acuminata* in its yellow, not *red*, corolla, etc. But the flower of *L. Loureiri* is of the same general colour as are the other Malaysian species: at first creamy or light yellow, later yellow. The other differential characters I think are of hardly any value for distinction. Specimens referred to this species are not present at Buitenzorg, but I do not hesitate in regard to its identity.

Lonicera philippinensis is represented at Buitenzorg by the two cited duplicates, which fit in clearly with the Javanese material. The small corolla, the tube as long as the limb, the dense umbelliform sessile inflorescences, the ciliate calyx, the short style, and the yellow pubescence point certainly to *L. Loureiri*, to which it should be reduced, in my opinion. Merrill says that it is quite distinct from *L. Rehderi*, but I cannot find any important difference after comparison of both descriptions.

Lonicera oxylepis Miq. is partly based on Blume's type. Miquel is of the opinion that the name *L. Loureiri* ought to be reserved for Loureiro's plant. This is not proper, since Blume's description was based wholly on Javanese specimens without any reference to Loureiro's plant, as was done by De Candolle.

Lonicera Leschenaultii Miq. non Wall. is clearly the same as *L. oxylepis*, as may be inferred from Miquel's publication.

Of *Lonicera acuminata* I have seen only the description and a sheet (*Smith & Cave 2633*) named *L. acuminata*, and two Sikkim sheets, coll. *T. Thomson*, named *L. Loureiri*, all of which are matched by several Javanese specimens (*Koens 444, Backer 3293, 3301, 21709*). Unfortunately, the specific name *L. acuminata* has priority over *L. Loureiri* by one year. On the other hand, Clarke also pointed to the identity and says that the Javanese species differs in the glabrous corolla-tube and style. I have found that these characters vary, the corolla is pubescent or glabrous, and the style is also sometimes pubescent on the middle portion (*Backer 25975*) or glabrous (*Backer 478*). Also the stamens are sometimes glabrous (*Backer 478*) or pubescent (*Bünnemeijer 891*). One must be very cautious in dissecting the stamens, otherwise their always hairy elongation which is coalescent with the corolla-tube is interpreted as "stamens with hairy base." If one is still convinced of the distinctive specificity of the Javanese specimens, the alternative is that *L. acuminata* also occurs in Java, the specimens from Java being identical with those from SE. Asia. The leaf-shape and size of the Javanese specimens vary from ovate to lanceolate.

Lonicera Giraldii Rehder is distinguished by Rehder from *L. acuminata* by a slight difference in the relation between the length of the tube and the limb, the size of the leaves, and the spreading hairs, characters which are rather variable. The only character of importance could be the spreading, not reflexed hairs of the corolla in *L. Giraldii*, but even this can hardly serve as a specific character.

Lonicera acuminata occurs in SE. Asia (Himalayas to China), the Philippines, and Sumatra-Java-Bali; it was dispersed in two invasions into Malaysia (FIG. 1).

5. **Lonicera pulcherrima** Ridl. (?*L. malayana* Henderson).

A species which can be easily distinguished in the subsection LONGIFLORAE by its pubescent style, the other species possessing this character being *L. sumatrana* (= *L. leiantha*), *L. Hildebrandiana, L. Braceana,* and *L. dasystyla*. From the first three it is totally different in its pubescence. From *L. dasystyla* it differs in numerous characters: the bracts as long as the ovary, the larger leaves yellow-tomentose (usually densely) beneath, the rich-flowered globose terminal inflorescence with flowers in subumbelliform clusters at the ends of the upper axillary stalks, and the hairy calyx-teeth which are as long as the ovary.

SUMATRA: Only in Atjeh, Tapanoeli, and the Eastcoast. Plant not tall, climbing mostly in open rocky places, between 850 and 1400 m. alt. — *Hagen s. n.*; *Huitema 50; F. R. I. b. b. 9842; Jochems 66; v. d. Koppel 8; Lörzing 4565, 4973, 6222, 6603, 7155, 7920, 8297, 9967*; *v. d. Meer Mohr 135*; *Ouwehand 66*; *van Steenis 5853*; *Symington 24690*; *Yates 1282, 1402, 2202.*

I can place *Lonicera malayana* here only provisionally until I have studied the type specimen; it is antedated by *L. pulcherrima* by one year. The large flowers (by corolla-tube 6 cm. long is probably meant the whole corolla statu vivo?) and the yellow pubescence remove it from

L. javanica and *L. acuminata*. Most characters, along with its geographical distribution and altitudinal range, point to its identity with *L. pulcherrima* Ridl. However, there are three points of difference: firstly the corolla is said to be *sparsely* yellow-pubescent on the outside (in *L. pulcherrima* it is densely or rather densely hairy), secondly, the style is mentioned as *glabrous* (Henderson may have overlooked the few hairs which are always present in *L. pulcherrima*), thirdly, the inflorescence is described "Peduncles axillary, 3 1/2 cm. long, . . . two-flowered." This hardly seems to match *L. pulcherrima*. A further decision is to be postponed.

Ridley correctly pointed out the difference between *L. macrantha* and *L. pulcherrima*.

6. **Lonicera javanica** (Bl.) DC. (*Caprifolium javanicum* Bl., ?*L. mindanaensis* Merr.) (Description after Javanese specimens).

Ultimate twigs *grey-short-hairy*, mixed with *glandular-tipped* hairs, the internodes soon *shiny brown, slender, 1.5–2 mm. diam.* Petiole *hairy, also in glabrate forms*. Underside of the blade *glaucous* (also s. s.), glabrate or more or less densely *grey-hairy* to thinly subtomentose. Margin of the blade flat or nearly flat. Upper surface of the blade *not or slightly rugose*, glabrous or the base of the midrib hairy. Inflorescences short *grey-hairy*, terminal and in the upper axils so as to form a rather *lax panicle exceeding the leaves*; lower branches up to 6 cm. long, provided with reduced leaves, the upper internodes not abbreviated, the flowers and stalks provided with numerous or few *glandular-tipped* hairs. Calyx-lobes *mostly* rather densely grey-hairy. Bud club-shaped, the thickened end about $\frac{1}{3}$–$\frac{1}{4}$ of the length of the mature bud, often acute. Corolla about *18–30 mm. long*. Corolla-tube *slender, about 1 mm. diam. or thinner*. Corolla-lobes *narrow*, about *1–2.5 mm. broad, both lips eventually recurved*, the lobes as long as the tube or *shorter*. Anthers thin, *2–4 × 0.3–0.5 mm.*, the stamens protruding. Style often *longer* than the corolla.

JAVA: *Backer 3700, 3702, 5215, 9861, 15710, 22496, 25087*; *Bakhuizen van den Brink 34, 1411, 1412, 2241*; *Danser 6737*; *Denker 48*; *Docters van Leeuwen 341*; *Kobus 141*; *Koorders 14939, 26033, 26300, 27917, 28647, 31617, 32270, 32891, 37356 — 37358*; *Lörzing 136*; *Mousset 641, 863*; *Sapiin 2561*; *Soegandiredja 185, 213*; *Smith & Rant 425*; *Winckel 775, 1857*.

BALI: *de Voogd 1680*.

Known only from Java, Bali, and the Philippines; closely allied to *L. glabrata* DC. and *L. affinis* Hook. & Arn.; in forests and forest borders between 1000 and 2000 m.; sometimes (in Java) cultivated.

On young shoots 3-lobed leaves sometimes occur (*Bakh. v. d. Br. 2241*). The leaf-parenchyma is very finely white-dotted in the herbarium under the lens. Sometimes 4-flowered clusters occur in the same plant along with 2-flowered cymes.

On the inflorescences, the leaves, and the internodes glandular-tipped hairs occur next to normal hairs. Sometimes the corolla is clad only with sparse glandular hairs. I have never seen sessile, red dot-like glands in *L. javanica* as in *L. pulcherrima*.

The pubescence is very variable. There is a series of intermediates between very hairy forms like *Koorders 14939* and almost glabrous forms

as collected by Rant above Prigeu and Ultée above Poenten. However, the petiole always remains hairy. Leaf-shape and leaf-size are also rather variable, with ovate and obovate leaves occurring on the same twig. The pubescence of the calyx-teeth varies from ciliation on the margin to entirely tomentose. The pubescence of the twigs and underside of the leaves may even approach a yellowish colour, e. g., in *Koorders 14939*, *26300*, *32891*. The hairs of the corolla are pointed downward, while the glandular hairs stand off at a right angle.

The length of the flower is variable, the tube 10–19 mm., the limb 8–14 mm. in the dried state (in living specimens the flower measures 30–35 mm.).

From *L. acuminata* it is easily distinguished by its slender, glandular corolla, the two recurving lips causing the stamens to protrude, and in the absence of rather stiff yellow hairs. Since in fresh specimens the corolla of *L. acuminata* measures from 15–30 mm., there is no reason to insert *L. javanica* in the subsection Longiflorae and *L. acuminata* (= *L. Loureiri*) in the subsection Breviflorae. The distinction of these subsections is in my opinion rather artificial, *L. javanica*, *L. affinis*, and *L. glabrata* being so closely allied that there is a chance that they will appear to belong to one species after an extensive study of more material.

Lonicera javanica has not been found as yet in Sumatra. To a certain degree it is replaced there by *L. pulcherrima*, but although *L. pulcherrima* grows at the same altitude, it prefers more open places and is, therefore, not such a tall climber as is usually the habit of *L. javanica*. I doubt whether the species really exclude each other.

Lonicera mindanaensis is a glabrate form (such as also occur in Java, though I have not found in Java entirely glabrous mature foliage as is described in *L. mindanaensis*), and the reddish brown branches, the small flowers, the hairy petiole, the narrow corolla-lobes, and the inflorescence point together to *L. javanica*. Merrill says that it is distinguished from *L. Rehderi* and *L. philippinensis* by its larger flowers. However, this difference hardly concurs with Merrill's description (*L. mindanaensis*: 22 mm. corolla; *L. Rehderi*: 20–22 mm.). *Lonicera mindanaensis* is described with filaments and style villous in their lower part, the bracteoles orbicular-reniform.

Doubtful records

Lonicera chinensis was mentioned as occurring in New Guinea by Miquel (Fl. Ind. Bat. 2: 128. 1856) on the basis of a specimen collected by Zippel to which the latter apparently had attached the manuscript name *L. repens* Zipp.

As *Lonicera* is not likely to occur in New Guinea, Zippel's specimen may represent a cultivated plant of *L. japonica*, but 1856 would seem a very early date for this ornamental. *Lonicera repens* is mentioned by Hasskarl as cultivated in the Botanic Gardens at Buitenzorg in his Cat. Hort. Bog., p. 116. 1844. According to Index Kewensis and Rehder this is *L. japonica*.

Though there is no reason for me to doubt Miquel's identification, an examination of the original specimen in the Leyden Herbarium is necessary. There is also a probability that Zippel's plant came from Java, as several of his labels appear to be incorrect or mislaid at Leyden; this was certainly not caused by that gentleman himself, as he was very accurate and of wide knowledge.

EXCLUDED RECORDS

Lonicera Gaertn. = Loranth.

Lonicera chinensis Wats., *L. confusa* DC., *L. javanica* DC., and *L. macrantha* DC. were mentioned to occur in the Philippines by F.-Villar, Nov. App. 104. 1880; these records are excluded by E. D. Merrill, Enum. Philip. Fl. Pl. 3: 578.

Lonicera Symphoricarpus Blanco, non L. = *Scurrula philippinensis* (Cham. & Schltd.) G. Don, cf. Danser in Philip. Jour. Sci. 58: 121. 1935.

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MEIOTIC PROPHASE PHENOMENA IN SPECIES AND INTERSPECIFIC HYBRIDS OF NICOTIANA

T. H. Goodspeed

With three plates and one text-figure

INTRODUCTION

Investigations bearing upon problems of species origins and relationships in the genus *Nicotiana* have been carried on in this laboratory at the University of California for many years. With increasing accumulation of evidence it appears that, in this genus at least, extent of chromosome pairing at MI in F_1 interspecific hybrids in general reflects the degree of relationship of the species involved. Recent articles (Goodspeed, 12, 13, 14) expose the extent and character of the data in this and other cytological connections and reveal the close correspondence between morphological, taxonomic, and cytogenetic evidence of relationships within the genus.

Chromosome behavior at MI has been studied in a total of 213 F_1 interspecific hybrids of *Nicotiana*. Information in the case of 135 of these hybrids, which involve as parents 53 of the 58 valid species (Goodspeed, 12, 14; Wheeler, 49), has been obtained in this laboratory, and Kostoff (27) has contributed much of the remainder. Of the 135, 69 are intrasectional, 25 intersectional, and 41 are intersubgeneric hybrids. Our evidence shows that 29 hybrids exhibit at MI complete or almost complete pairing, 35 lack of pairing or approximations thereof, 22 low but variable pairing, 16 high but variable pairing and 35 "Drosera scheme" pairing. Examples of these various categories of pairing are discussed in what follows.

The correlation of extent of MI pairing in hybrids with the taxonomic relationships of the species involved is as follows: in approximately 90% of intrasectional hybrids pairing is complete or nearly so; 90% of intersectional and all intersubgeneric hybrids fall into the lack of pairing category; all hybrids involving amphidiploid species (cf. Goodspeed and Bradley, 16) and the descendants of their putative ancestors show "Drosera scheme" pairing, while 85% of hybrids involving these amphidiploid species and species other than those postulated to have entered into their parentage show almost complete lack of pairing. The information concerning meiotic phenomena in the additional 78 hybrids studied by others enforces almost without exception the significance of the above evidence.

The proposition that amount and character of MI pairing reflects the extent to which in the parental genoms the genes and their arrangement are

the same or similar is obviously basic to all cytotaxonomic conclusions to which studies of first meiotic metaphase chromosome behavior contribute (Stebbins, 44). A considerable to a high degree of MI pairing is characteristic of many interspecific hybrids in most genera other than *Nicotiana* (cf. Stebbins, l. c.). The apparent conclusion that *Nicotiana* is unique in the sense that many interspecific hybrids exhibit a negligible amount of MI pairing is, however, difficult to document. Taxonomic criteria from genus to genus are variable, and thus what is said to constitute an interspecific hybrid in one may correspond to a varietal hybrid in another. Again, in no other genus is comparable cytological evidence available for such a high proportion of the possible interspecific combinations, and there is here the suggestion that more extensive data for other genera might reveal the occurrence of pairing categories comparable to those in *Nicotiana*. This discrepancy in evidence may be, in part at least, a product of inability to obtain interspecific hybrids in other genera, a possibility which suggests that the ability to obtain numerous hybrids between species of *Nicotiana* which are taxonomically remotely related may be due to evolution of factors inhibiting crossibility having occurred at a slower rate than evolution of those responsible for species differentiation. In any case, interspecific hybridization — frequently leading to amphidiploidy with its polyploid and aneuploid byproducts — apparently represents a major evolutionary mechanism in *Nicotiana*, and disappearance of many of the contributory ancestors leaves the modern genus small in terms of species and restricted in terms of distribution. In such a relic genus with such an evolutionary background species distinctions, morphological and thus genic, may be expected to be considerable with the result that lack of pairing and "Drosera scheme" pairing are of relatively frequent occurrence among its F_1 interspecific hybrids. In other words, it is probable that *Nicotiana* may actually be unique among genera which have been cytotaxonomically treated.

Important for the interpretation of the character and significance of MI pairing in F_1 interspecific hybrids is the question of the extent to which pairing observed at MI is a reflection of meiotic prophase association. This is particularly true, for example, in the considerable number of *Nicotiana* hybrids where the pairing mode at MI is zero or approximately zero. It may be contended in such cases that MI evidence is not reliable because genic effects are known to produce desynapsis and thus a complete or considerable zygotene-pachytene association might not necessarily be followed by the appearance of a corresponding amount of MI pairing. Therefore, without evidence concerning early meiotic prophase phenomena in hybrids, the amount of MI pairing is doubtfully applicable to interpretation of the relationships of the parental species involved. In the present article the results of comparative studies of meiotic prophases of species and F_1 interspecific hybrids of *Nicotiana* are described and commented upon.

There are few reports of meiotic prophase phenomena in species or F_1

interspecific hybrids of *Nicotiana*. For triploids of *N. tabacum* Olmo (35) and for haploids of that species, Lammerts (28) described the extent and something of the character of pachytene associations. In a normal haploid plant the average number of bivalents per PMC at MI ranged from .17 to .43, while in a "Coral" *N. tabacum* haploid in which the F chromosome was genetically altered the average was 1.44. At pachytene the correspondingly greater amount of association observed in the "Coral" as contrasted with the normal haploid was assigned primarily to non-homologous pairing. In an asynaptic haploid of *N. sylvestris* (Goodspeed and Avery, 15), approximately 50% of the PMC contained a bivalent at MI with some instances of 2 to 4 bivalents. Some pachytene pairing was seen, primarily between segments of two strands which apparently were structurally alike as a result of duplication. The rare occurrence of more than one bivalent at MI was assigned to non-homologous association and "fold backs" at prophase. In the above citations emphasis at pachytene was laid upon correspondence in chromomere pattern or its absence as indicative of the presence or lack of homology in the paired chromosomes. Some reference to meiotic prophase in haploids of *N. rustica, N. Langsdorffii*, and *N. sylvestris* is made by Kostoff (27), who found that the negligible amount of pairing observed at MI was preceded by a minimum amount of pachytene association. Elvers (9) made a preliminary examination of pachytene in F_1 *N. glutinosa* $\times$ *N. wigandioides*.[1] At MI this hybrid shows a range of 2 to 9 pairs. At pachytene paired threads appeared to be much more numerous than unpaired ones. In some cases Elvers considered the paired threads homologous in terms of matching chromomeres, while others appeared to be instances of non-homologous association.

Relatively little information is available concerning the relation between prophase and MI chromosome behavior in hybrids in other genera in which pairing at the latter stage of meiosis is lacking or reduced. In most such cases a typical pachytene stage was not seen (cf. Federley, 10; Harrison and Doncaster, 17; Ramanujam, 37) or only short paired segments were observed (Meurman, 32). However, Karpechenko (21) found in hybrids of *Raphanus sativa* $\times$ *Brassica oleracea* that synapsis did not differ from that in the parents, although there was no pairing at MI. In an interspecific hybrid in *Crepis* (Tobgy, 48), marked differences in length at MI of the parental chromosomes apparently did not reduce the extent of pachytene association.

The reduced amount of MI pairing in asynaptic and desynaptic plants makes them in that sense comparable to F_1 interspecific hybrids of *Nicotiana* which show lack of or low variable pairing. In desynapsis more or less normal zygotene association is observed or indicated (cf. Koller, 23) to have occurred and is followed by lack of chiasma formation (cf. Beadle,

[1] Not F_1 *N. glutinosa* $\times$ *N. tomentosa* as originally reported by Elvers.

2; Catcheside, 5; Levan, 29), while in asynapsis zygotene association is found to be lacking or at a minimum (cf. Huskins and Hearne, 19; Ramaer, 36; Yamomoto, 51). Both phenomena are taken to be genically controlled. The falling apart of chromosomes was seen to occur in late pachytene or between diakinesis and MI (cf. Richardson, 39; Levan, 29; Li, Pao, and Li, 30).

TECHNIQUE

Variations of the conventional paraffin technique did not give adequate pictures of meiotic prophase conditions in PMC of species or F_1 interspecific hybrids of *Nicotiana,* although certain paraffin preparations were useful for comparative purposes. Smears were satisfactory when prepared according to the following techniques:

A. After fixation in 3 parts absolute alcohol to 1 part glacial acetic acid for 20 to 24 hours, the anthers were removed to 70% alcohol, two or three changes of alcohol being made within a period of a few hours. A shorter (12 hour) fixation did not prove to be so satisfactory.

B. Fixation in 1 part chloroform to 1 part of the solution used in fixation A was continued for 24 hours to several days. Anthers transferred to alcohol after a 24 hour fixation showed darker cytoplasm than those left in the fixative for a considerably longer period.

After fixation anthers were smeared in strong iron aceto-carmine. Additional iron from dissecting needles was added to the drop of carmine in which anthers were to be smeared until the stain began to appear purplish. Preparations were alternately heated and pressed until the desired degree of spreading and staining of the chromosomes was achieved. Technique B proved to be superior to technique A for detailed studies of spiralization in loops and segments of chromosomes. The less delicate quality of the staining in technique A, however, made its use more appropriate for investigation of the entire contents of nuclei. Therefore, all drawings except PLATE I, *fig. 6* were made from material prepared according to technique A. Swanson (46) has had success in demonstrating finer structure of early prophase chromosomes in *Tradescantia* after pretreatment with heat. One set of cut inflorescences of several *Nicotiana* species was, therefore, kept in jars of water at approximately 40°C. for 24 hours and another at 32°–35°C. for the same period. In neither case did the results of such pretreatment improve the definition of prophase in our material.

OBSERVATIONS

(a) SPECIES. — Over a period of years information has accumulated in this laboratory concerning diplotene-diakinesis sequences in *Nicotiana* and has been applied to interpretation of chromosome behavior at MI in species and F_1 interspecific hybrids. Until the techniques above described were available, pre-diplotene stages proved difficult to study and little significant evidence on those early meiotic phenomena was secured.

The four species referred to in what follows were selected for description of the leptotene-diakinesis progression because they are distinguished from one another in chromosome number or karyotype or because they represent parents of F_1 hybrids in which meiotic prophases have been studied. Members of Subgenus *Petunioides*, Section *Alatae*, *N. Langsdorffii* (n = 9) has a $2\ m + 4^1\ s\ m + 3^1\ st$ karyotype and *N. longiflora* a $10^2\ st$; *N. glauca* (Subgenus *Rustica*, Section *Paniculatae*) has a $1m + 1\ s\ m + 10^1\ st$ karyotype, while in *N. otophora* (Subgenus *Tabacum*, Section *Tomentosae*) the karyotype is $7^1\ m + 5^1\ st$ (Goodspeed, 13). In a number of instances marked distinctions in somatic chromosome morphology make possible the identification of individual chromosomes in early meiotic prophases and thereby assist in interpretation of the results obtained.

Pre-leptotene chromosomes show relic coils which are eliminated by mid-leptotene along with parallel enlargement of the nucleus and lengthening of individual strands. Adequate evidence of duality and of the relational coiling of sister chromatids resulting from a gradual resolution of relic coiling is not yet available. Optically, therefore, mid-leptotene chromosomes appear as much attenuated, slender chromonemata evenly distributed in the nucleus. With technique A these chromosomes have a distinctly beaded appearance which for certain of them at least seems to correspond to a pattern in terms of size and linear position of chromomeres. With technique B, however, equivalent material shows the establishment at mid-leptotene of the meiotic spiralization cycle. Thus it appears that the beaded appearance of the chromosomes (chromomeres) is largely a product of fixation which obscures the presence of the major spiral without altering spiralization patterns. The "spiralization pattern" of a meiotic prophase chromosome is here assumed to be established by genically controlled distinctions in size and pitch of gyres, in their linear relations, and in amount and/or character of nucleic acids of consecutive segments. In other words, our evidence supports the conclusion that a pattern of chromomeres represents a heritable spiralization pattern. From this point of view the spiralization pattern is the same in sister chromatids and homologous chromosomes. Certainly at zygotene conspicuous linear correspondence of spiralization patterns is often seen, and obviously complete and intimate association between two chromosomes in which the major coils have been developed can occur only where both possess identical spiralization patterns.

At early zygotene conjugating segments are seen at ends of chromosomes and/or in intercalary regions which may represent position of centromeres (PLATE I, *fig. 6a, b*). Free ends extending from paired segments frequently can be seen to possess identical spiralization patterns. By late zygotene intermeshing of the two spiralized chromosomes is complete and only at ends (particularly at satellites) can the dual nature of the strands be demonstrated. Some relational coiling occurs at pachytene and appears to represent random twisting of the long paired threads. During pachytene appreciable condensation is seen. This is a product of the onset of

despiralization which begins to be conspicuous at late pachytene, where in chromosomes undergoing repulsion the number of gyres is reduced, the diameter of the gyres is increased, and the gyres are closer together (PLATE I, *fig. 6 c, d*).

At mid-pachytene distinctions in somatic chromosome morphology within the genoms of the species of *Nicotiana* under discussion permit identification of entire paired lengths or large segments of such lengths. Thus, in a number of PMC of *N. Langsdorffii* four of the nine pairs can be individually distinguished (cf. PLATE I, *fig. 2*). For example, the entire extent of one submedian pair characterized by possession of an extremely large satellite, and of one very short subterminal pair with distal satellites, could be studied and were found consistently associated with the nucleolus. In this species at pachytene centromeric as well as satellite constrictions are pronounced and usually reflect the duality obtaining. In *N. longiflora* (PLATE I, *fig. 3*) the two chromosomes which bear satellites, one a small proximal and the other a large distal satellite, and the nucleolus were always associated. Even at this stage these two chromosomes were distinguishable from each other by reason of size and position of satellites. Another somatic chromosome of this species characterized by a large distal knob is readily identifiable at pachytene by the presence of a conspicuous terminal heterochromatic area. Although during mitosis the knob never appears as a typical satellite it is at pachytene frequently, though not consistently, found near the nucleolus. In *N. longiflora* centromeric constrictions at pachytene, unlike those of *N. Langsdorffii,* are not pronounced in the majority of the chromosomes. As in *N. Langsdorffii* and *N. longiflora,* so also in *N. glauca* (PLATE I, *fig. 1*) and *N. otophora* certain chromosomes at pachytene can be identified by distinctions in centromere position and/or by number and size of satellites, and in the latter species certain chromosomes of both length classes of the strikingly dimorphic genom can be followed over their entire extent.

In early diplotene condensation has reached the point where, in such species of low chromosome number as *N. Langsdorffii* and *N. longiflora* (PLATE I, *fig. 4*), the majority of the paired lengths can be studied in their entirety. However, relational coiling due to twisting of homologues makes impossible a determination of all points at which crossing-over has occurred. As diplotene advances, further despiralization, accompanied by maximum attraction and repulsion of homologues and chromatids, is apparent with consequent decrease in relational coiling. As a result chiasmata in the now optically quadripartite units become readily distinguishable from twists which did not involve crossing-over (PLATE I, *fig. 4*). Often chromatids can be traced through chiasmata and the independent coils of sister chromatids identified (PLATE I, *fig. 6 g*). At diakinesis (PLATE I, *fig. 5*) the tetrads, distributed about the periphery of the nucleus, become exceedingly compact and are characterized by outlines the distinctly uneven

quality of which indicates the presence of spiralization which is obscured by accumulation of matrical material.

(b) Hybrids. — In all F_1 interspecific hybrids of *Nicotiana* except those characterized by approximately complete MI pairing the meiotic prophase sequence, particularly mid to later stages, shows marked departures from that of the parental species, the extent of the distinctions being in general directly proportional to the extent to which the chromosomes fail to pair at MI.

As in other genera, the leptotene-diakinesis sequence in species of *Nicotiana* exhibits stages which become points of reference. Thus, zygotene with its tendency toward parallel orientation of homologues and its evidence of the beginning of synaptic unions, mid-pachytene where all chromosomes exhibit an approximately uniform degree of condensation and are completely paired with duality apparent only at ends or where repulsion is already under way, and diplotene with its conspicuous configurations can all be identified with confidence. By contrast, in F_1 interspecific hybrids such points of reference may be much less pronounced or entirely lacking. For example, in hybrids of the lowest pairing category there is nothing comparable to zygotene, pachytene is identifiable only in PMC where certain chromosomes show intimate association over relatively short segments, and typical diplotene does not occur.

In hybrids, as in species, pre-leptotene chromosomes exhibit relic coiling. As leptotene strands take form, this coiling is wholly or largely lost and by mid-leptotene appears to be replaced by the initiation of the new major coiling cycle. As in species, the leptotene material of hybrids prepared according to technique A showed bead-like chromomeres which after technique B was applied to equivalent material were seen as gyres of a specific spiralization pattern. Although not yet adequately demonstrated, it appears that in hybrids, particularly of the low pairing category, there is a somewhat stronger suggestion than in species of duality of early to mid-leptotene chromosomes. Assuming leptotene duality, relational coiling of sister chromatids resulting from straightening of relic coiling must have been eliminated, probably, in part, by rotation of ends in the enlarging nucleus and in part by the initiation independently in the closely appressed sister chromatids of the major coiling cycle. In general, except for absence of typical zygotene, pre-pachytene conditions in hybrids correspond to those in species.

At pachytene, however, striking contrasts appear. Whether pachytene pairing in a given nucleus of a hybrid is approximately complete or is limited to a few short segments or is entirely lacking, the unpaired chromosomes (whole chromosomes or segments) are strikingly atypical as a result of the occurrence of alternating thick and thin areas of varying length. This phenomenon continues until diakinesis which, apart from differences in the valencies of the chromosomes involved, is entirely comparable in appearance to the same stage in species. The presence of spiralization

patterns in the chromosomes throughout the meiotic prophase is more readily demonstrated in hybrids than in species, at least in the sense that it is revealed after technique A as well as after B.

As a typical representative of a *Nicotiana* hybrid exhibiting lack of pairing at MI, the meiotic prophases of F_1 *N. glauca* ($n = 12$) × *N. plumbaginifolia* ($n = 10$) were extensively studied (PLATES II, III). Apart from the report of Kostoff (27), more than 4 pairs at MI have not been seen in this hybrid. Some 750 PMC analyzed by Ramanujam and Joshi (38) gave a pairing range of 0 to 4, well over 75% showing zero pairs, and our unpublished data involving over 100 PMC correspond (*Text fig. 1, a*). On the other hand, Kostoff (l. c., p. 396) reports a pairing range of 3 to 9 and elsewhere (l. c., p. 632) one of 6 to 10. It should be noted that the occurrence of numerous "off-spindle attachments" and the tendency of the univalents to form an equatorial plate rather than lying scattered in the PMC produces a misleading impression of the amount of pairing obtaining.

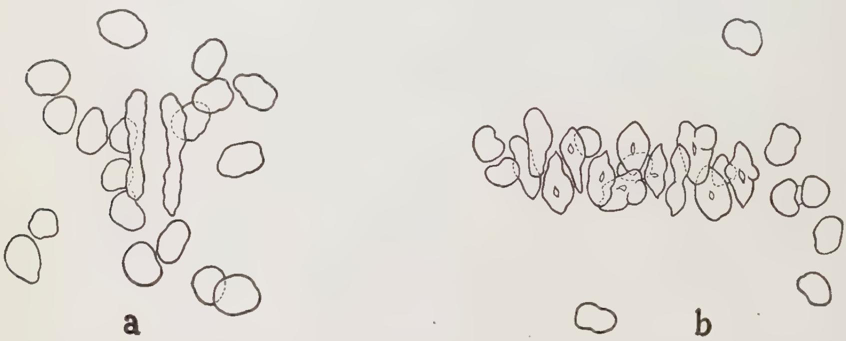

FIG. 1. MI conditions in F_1 interspecific hybrids: *a*, F_1 *Nicotiana glauca* (n = 12) × *N. plumbaginifolia* (n = 10), showing 2 bivalents and 18 univalents, off-spindle attachments, and secondary association; *b*, F_1 *N. tabacum* (n = 24) × *N. otophora* (n = 12), showing 12 bivalents and 12 univalents.

In this hybrid some PMC at a stage taken to correspond to pachytene showed only unpaired chromosomes, but in the majority of PMC from one to several paired segments, frequently but not exclusively terminal, occurred (PLATE II, *figs. 2, 3*). Usually such paired segments were short, but in most favorable material a relatively long paired segment was sometimes seen.[2] In terms of identity of spiralization patterns of the segments paired at pachytene and of distinctions of such patterns in unpaired segments of the same chromosomes, conjugation appears to occur only between structurally homologous segments of otherwise non-homologous chromosomes (PLATE II, *fig. 3*). This conclusion is borne out by the occasional presence of heteromorphic pairs at MI in this hybrid.

[2] Undoubtedly this pairing is of sufficient length to permit chiasma formation, a fact which probably accounts for the relatively frequent occurrence of one pair at MI.

At diplotene (cf. Plate II, *figs. 4, 5, 6*) the duality of each chromosome is rather strikingly visible, particularly in terminal areas (Plate II, *fig. 5*), sister strands showing as independently coiled elements capable of lateral separation from each other. At early diakinesis (Plate III, *fig. 1*) evidence of duality and spiralization is unmistakable, whereas in species at an equivalent stage both are somewhat difficult to demonstrate. In the hybrid centromeric constrictions are conspicuous. Frequently the initiation of off-spindle attachments and of secondary association characteristic of some univalents at MI can be seen (Plate III, *fig. 2*), reflecting perhaps an earlier association of segments too short to permit chiasma formation.

In the case of F_1 *N. tabacum* (n = 24) × *N. otophora* (n = 12), a hybrid which combines the genoms of the former species and of a modern descendant of one of its putative ancestors, MI shows a close approximation of the "Drosera scheme" pairing which is characteristic of other hybrids which, like it, involve amphidiploid species and those related to their parentage. The pairing mode in some 150 PMC analyzed is $12_{II} + 12_{I}$ although a range of 10 to 13 pairs occurs, with a trivalent frequently seen (*text fig.* 1, b). As in F_1 *N. glauca* × *N. plumbaginifolia,* a lack of pairing hybrid, detailed prophase studies of this "Drosera scheme" one reveal a complete correspondence between the amount of pachytene and MI conjugation (Plate III, *figs. 3, 4, 5*). Thus at the former stage paired and unpaired chromosomes appear in approximately a 1:1 ratio (Plate III, *fig. 3*), although it cannot be determined as accurately as can the MI ratio of bivalents to univalents because of the difficulty of following any one of the pachytene chromosomes throughout its entire length. However, complete pairing is clearly visible over the entire extent of large pachytene loops which, in some instances at least, represent the major portions of the chromosomes involved, and the occurrence of long unpaired lengths is equally conspicuous. Unpaired segments in otherwise completely paired strands are seen at times. In them the spiralization patterns are not the same, whereas paired chromosomes consistently appear to be structurally homologous. Some relational coiling of homologues was observed.

As will be noted in Plate III, *fig. 3,* satellited chromosomes — two paired and one unpaired — are attached to the nucleolus, and there are not too sharply defined heterochromatic regions, the latter doubtless contributing the chromocenters which are peculiarly conspicuous in somatic nuclei of *N. otophora* at the metabolic stage.

Pairing at MI in F_1 *N. paniculata* (n = 12) × *N. Benavidesii* (n = 12) is approximately as complete as it is in the parental species with a mode of 12_{II} in 85 of the 100 PMC analyzed. At pachytene, in the many cells examined, no unpaired chromosomes or segments were found. Another hybrid of the complete pairing category, F_1 *N. Raimondii* (n = 12) × *N. cordifolia* (n = 12), is important as indicating the degree of reflection of MI conjugation at pachytene, since at MI the pairing mode is $11_{II} + 2_{I}$ and in pachytene, although completely paired lengths are the

rule, unpaired segments can at times be seen. Throughout the meiotic prophase sequence of the complete pairing hybrids all stages appeared to correspond in detail to equivalent stages in the parental species.

For the hybrid F_1 *N. tabacum* (n = 24) × *N. glauca* (n = 12) the extent of MI pairing has been variously reported. Sarana (41) mentions "up to 12 pairs," Kostoff (27) gives a pairing range of 9 to 12, while in approximately 100 PMC analyzed here the range was 0 to 8 with 4 and 5 pairs occurring with equal frequency. This hybrid has therefore been placed in the low variable pairing category and prophase investigation makes it clear that association at pachytene is similarly low but variable in amount. Although unpaired chromosomes predominate in the majority of the PMC there is considerable variation from one cell to the next, but no instance of "Drosera scheme" or even approximately "Drosera scheme" pairing occurs.

Prophase conditions in an asynaptic individual of *N. tomentosa* (n = 12) were studied, since under the influence of environmental conditions variability in extent of MI pairing was comparable to that of such a hybrid as has just been described. When pachytene and MI material were taken simultaneously from this plant the latter stage was a reflection of the former in terms of the amount of pairing which occurred. It should be noted, however, that even when MI pairing was minimum the majority of PMC at pachytene showed, by contrast with F_1 interspecific hybrids of *Nicotiana* of the lack of pairing category, a considerable number of paired segments and even what were taken to be one or more completely paired chromosomes (cf. PLATE III, *fig. 6*).

COMMENT AND SUMMARY

Comparative studies of meitoic prophase phenomena in species and F_1 interspecific hybrids of *Nicotiana* above described show that in both cases the extent and quality of MI pairing is a reflection of the amount of early prophase association. Thus, in a hybrid showing approximately as complete pairing at MI as occurs in the parental species, zygo-pachytene conjugation is also complete. In a hybrid exhibiting a variable amount of pairing from one PMC to the next at MI, an equivalent range in ratio of paired to unpaired chromosomes appears throughout the zygotene-diakinesis sequence. Similarly, where "Drosera scheme" behavior is shown at MI in a hybrid where the chromosome number of one parent is twice that of the other, the ratio at pachytene between paired and unpaired units is approximately 1:1. The extensive studies of prophase phenomena in hybrids showing complete or almost complete lack of pairing in all PMC analyzed at MI confirm the evidence just summarized that univalents at MI reflect absence of prophase association or that such association is commonly confined to short segments.

There is no evidence that genically conditioned desynapsis is responsible

for the univalents present at MI in F_1 interspecific hybrids[3] nor that their occurrence can be assigned to the presence of an inherited asynaptic state. If a genic alteration causing asynapsis is recessive, its effects would not be manifest in the hybrids under discussion. It is, of course, possible that dominant gene mutations leading to asynapsis might offer an explanation for a few of the many instances of complete lack of pairing or variable pairing at MI, but "Drosera scheme" behavior obviously could not be assigned to the operation of such heritable influences. Furthermore, the fact that distinctions in relationship based upon morphology and distribution are almost uniformly in accord with cytogenetic evidence is significant in this entire connection.

Chromomeres have been variously described and interpreted. For example, they have been referred to as discrete chromatic disks of varying thickness (Heilborn, 18), as a series of enlargements of the genonema (Koltzoff, 25), condensation centers of chromatin (Ellenhorn, 8), localization centers of nucleic acids (Caspersson, 4), products of close intertwining of sister chromatids (cf. Kaufmann, 22), and as misinterpretations of coiled structures (Ris and Crouse, 40). In *Nicotiana* interpretation of chromomeres and their disposition as evidence of the presence of specific spiralization patterns appears justified. As already indicated a spiralization pattern is here taken to represent the product of genically controlled distinction in size and pitch of gyres, in their linear relations, and in the quantity and character of nucleic acids in consecutive segments.

In the species of *Nicotiana* examined leptotene duality is not demonstrable. However, at lepto-zygotene each chromosome is here assumed to represent a double strand the sister chromatids of which have been freed from relational coiling by rotation as they earlier straightened and lengthened and by initiation of the major coil independently in each chromatid. Onset of spiralization at leptotene is suggested by the evidence of Taylor (47), Shinke (43), Koshy (26), Naithani (34), and Swanson (46), whereas Darlington (7) and Huskins and Smith (20) see leptotene as unspiralized.

Following zygotene intermeshing of chromosomes, the homology of which determines an identity of their spiralization patterns, the pachytene-diakinesis sequence becomes a product of despiralization, the operation of forces of repulsion and attraction and the addition of nucleic acids, each of these phenomena characterized by its specific timing relation to the complete progression. Despiralization beginning in pachytene is visible at late pachytene in the greater diameter, as compared with zygotene, of the separating chromosomes and continues through diplotene (Plate I, *fig. 6e, f*) and diakinesis to effect a progressive decrease in number of gyres and increase in their diameter. This evidence for *Nicotiana* agrees with Swanson's (46) conclusion for *Tradescantia* but is in contrast to that of

[3] Such "desynapsis" as occurs corresponds only to the falling apart of short segments associated at pachytene in which the homology does not extend over a sufficient distance to favor chiasma formation.

certain investigators who see indication of comparable despiralization only at a considerably later stage. The assumption that despiralization is beginning independently in each chromatid of the tetrad during pachytene, concurrently with the occurrence of crossing-over and chiasma formation between chromatids of homologues, suggests that the breaks which condition the latter phenomenon may be in part a result of the tensions set up by the former process. This same assumption provides an explanation of the observed reduction in relational coiling of homologues, decrease in chiasma frequency, and increase in terminalization coefficient characteristic of diakinesis as contrasted with diplotene (Swanson, 45). It appears that the degree of despiralization observed is sufficient to account for the amount of reduction in length of strands which is seen between pachytene and diakinesis without employing axial contraction of the chromosomes as a contributing factor. In *Nicotiana* there is during prophase no evidence of the minor coil which is referred to elsewhere and considered (cf. Sax, 42) as a third factor in effecting reduction in chromosome length.

To analysis of the factors involved in the progress from leptotene to diakinesis, the study of prophases of hybrids, particularly those of the lack of pairing category, makes contributions. As shown above such material where the parental chromosome numbers are low is peculiarly valuable for interpretation of spiralization phenomena. The unpaired chromosomes of both the hybrids and the asynaptic under discussion consistently exhibit striking distinctions in the width of alternating segments (of varying length), a condition undoubtedly proceeding from a disruption of the timed progression of the spiralization-despiralization cycle characteristic of normal species. Investigations of similar material in other genera reveal prophase irregularities. For example, in asynaptics Huskins and Hearne (19) refer to a "confused irregularly contracted zygotene-diakinesis condition," Beadle (1) refers to "local regions of greater condensation," and Ramaer (36) to "a mass of threads partly contracted . . . . " Similarly for F_1 hybrid prophases reference is made to "many fine threads with thickenings at some places . . . [perhaps] the result of differential contraction of threads" (Ramanujam, 37), "general thickening of threads with irregularly alternating regions becoming attenuated and strained in appearance" (Melburn, 31), to the fact that in some loops very thin regions connect thick ones (Cretschmar, 6), and that "the chromosomes undergo successive changes at different rates" (Meurman, 32). Lack of uniform timing of despiralization appears, in large part, to account for the presence in *Nicotiana* hybrids and in an asynaptic of alternating thick and thin segments of varying length in the unpaired chromonemata. Thus, precocious despiralization produces increased width in one segment while segments of the same chromosome retain their relatively attenuated pre-pachytene appearance. In PLATE II, *fig. 4* the presence of a coil with gyres varying in diameter and degree of relaxation can be seen.

There is probably a relation between the timing of the spiralization-

despiralization cycle and the progression of nucleic acid condensation during prophase. For example Callan (3) concludes that nucleic acid is always present during spiralization, White (50) suggests that since chromatids are regarded as more tightly coiled at metaphase when the nucleic acid concentration is taken to be at a maximum, spiralization may be a consequence of nucleic acid synthesis, and Goldschmidt and Kodani (11) refer to coiling or molecular folding of the chromonemata forming the core of the disks of salivary gland chromosomes and to the presence of nucleic acid in the disks and its probable absence between them. It is, therefore, possible that disruption of normal spiralization-despiralization in hybrids might fundamentally represent a disruption of the normal nucleic acid cycle. In this connection it is to be noted that the nucleolus may be concerned in nucleic acid metabolism (cf. Koller, 24), and presumably the balance between the rôles played by nucleoli, chromosomes, and plasma is a specific character. If this is the case, the presence of nucleoli of unrelated origins, and thus presumably of distinctions in amount and activity of nucleolar material, in the nucleus of an interspecific hybrid might directly influence the nucleic acid cycle. Indeed, the physiological condition of the hybrid protoplast as a whole, which is the product of interaction of often large distinctions in the genic constitution of the parental genoms, might affect nucleic acid synthesis. Since in species of *Nicotiana* at pachytene, areas known to be heterochromatic because of connection with centromeres show only a slight differential reaction to staining, the distribution of heterochromatin may not be limited to centromeric regions and satellites (cf. Morgan, Schultz, and Curry, 33). Thus, the thicker and denser portions of the chromosomes above referred to as characteristic of prophases of lack of pairing hybrids might be related to distinctions or transitions between eu- and heterochromatin or, at least, the presence of such chromatic distinctions might intensify the appearance of disruption of the normal pachytene-diakinesis sequence.

The above interpretation of prophase phenomena in F_1 interspecific hybrids of *Nicotiana* has introduced a series of problems which require for solution more evidence than is at present available. Irrespective of the significance which may attach to these phenomena in terms of spiralization-despiralization, nucleic acid and heterochromatin cycles or states, the importance of the results of the comparative prophase studies above described lies in their application to the relation between MI pairing and prophase association. As already stated, the significance of MI association in terms of its indication of fundamental relationships between the parents of F_1 interspecific hybrids cannot be fully accepted without evidence from preceding prophases that such pairing or its lack reflects synapsis or its absence. The investigations discussed above supply such evidence. Therefore, on the basic assumptions concerning the factors responsible for synapsis, it appears that the amount of MI pairing in interspecific hybrids, of *Nicotiana* at least, may be taken as a measure

of the degree to which the genes of the parental genoms united in those hybrids are equivalent or similar in character and arrangement. In other words, in *Nicotiana* the extent and quality of MI association represents a reliable cyto-taxonomic criterion suggestive of phylogenetic relationships.

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EXPLANATION OF PLATES

All figures drawn with camera-lucida and reduced to × 1360.

PLATE I

Meiotic prophases of species of *Nicotiana*.

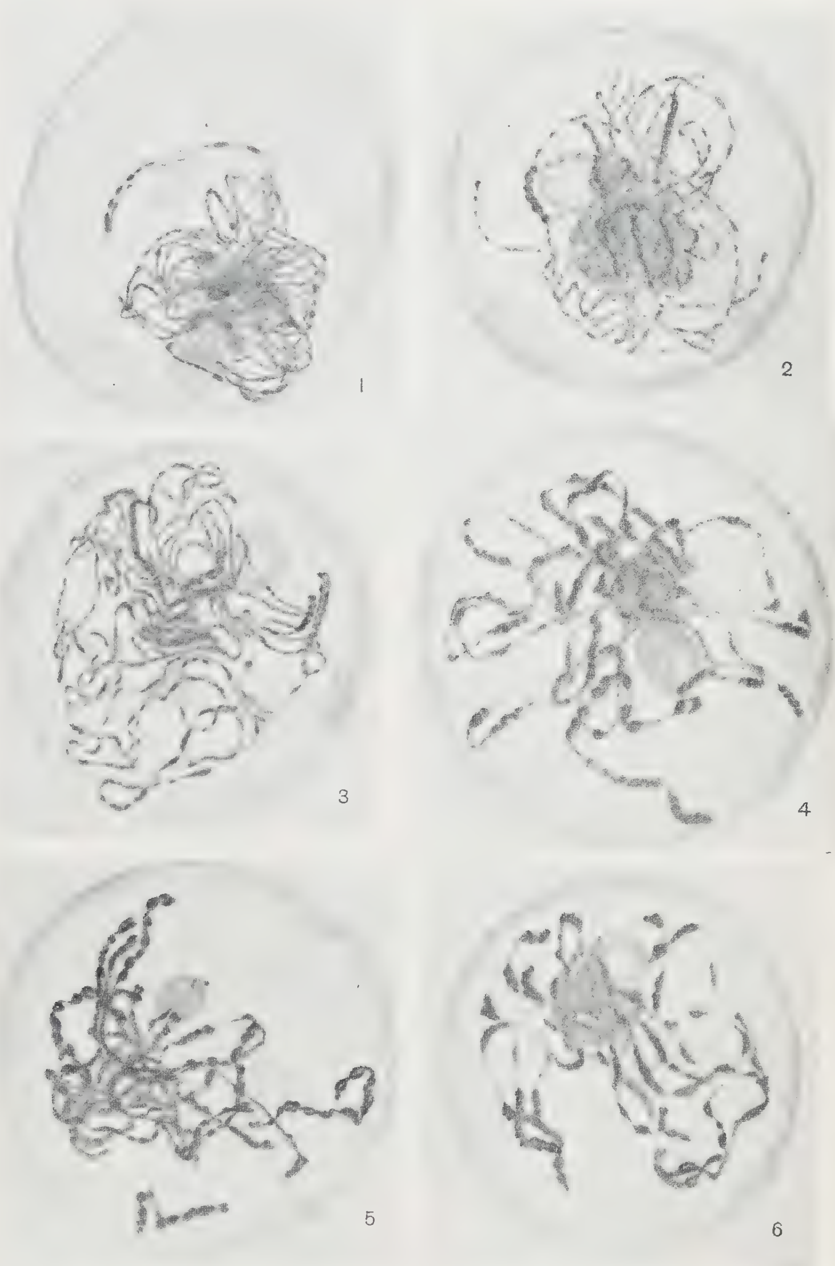
FIG. 1. Pachytene, *Nicotiana glauca* (n = 12): paired chromosomes exhibiting duality at ends and centromeres. FIG. 2. Pachytene, *N. Langsdorffii* (n = 9): four pairs distinguishable in their entirety — two satellited, one long *m* (above), and one *st* (near nucleolus). FIG. 3. Pachytene, *N. longiflora* (n = 10): two satellited pairs associated with nucleolus, another with distal knobs near nucleolus. FIG. 4. Diplotene, *N. longiflora*: all pairs distinguishable throughout their lengths; structure of some chiasmata visible. FIG. 5. Diakinesis, *N. longiflora*. FIG. 6. Zygotene to late diplotene (segments), *N. Langsdorffii*. (*a*), (*b*) zygotene: (*a*) pairing practically complete; (*b*) pairing in centromere area. (*c*), (*d*) pachytene showing onset of despiralization: (*c*) in homologues; (*d*) in segment (including centromere) of pair with large satellite. (*e*), (*f*) early diplotene: identity of spiralization patterns (*f*) in repulsed segment. (*g*) later diplotene: structure of chiasmata and character of spiralization in an entire chromosome pair.

PLATE II

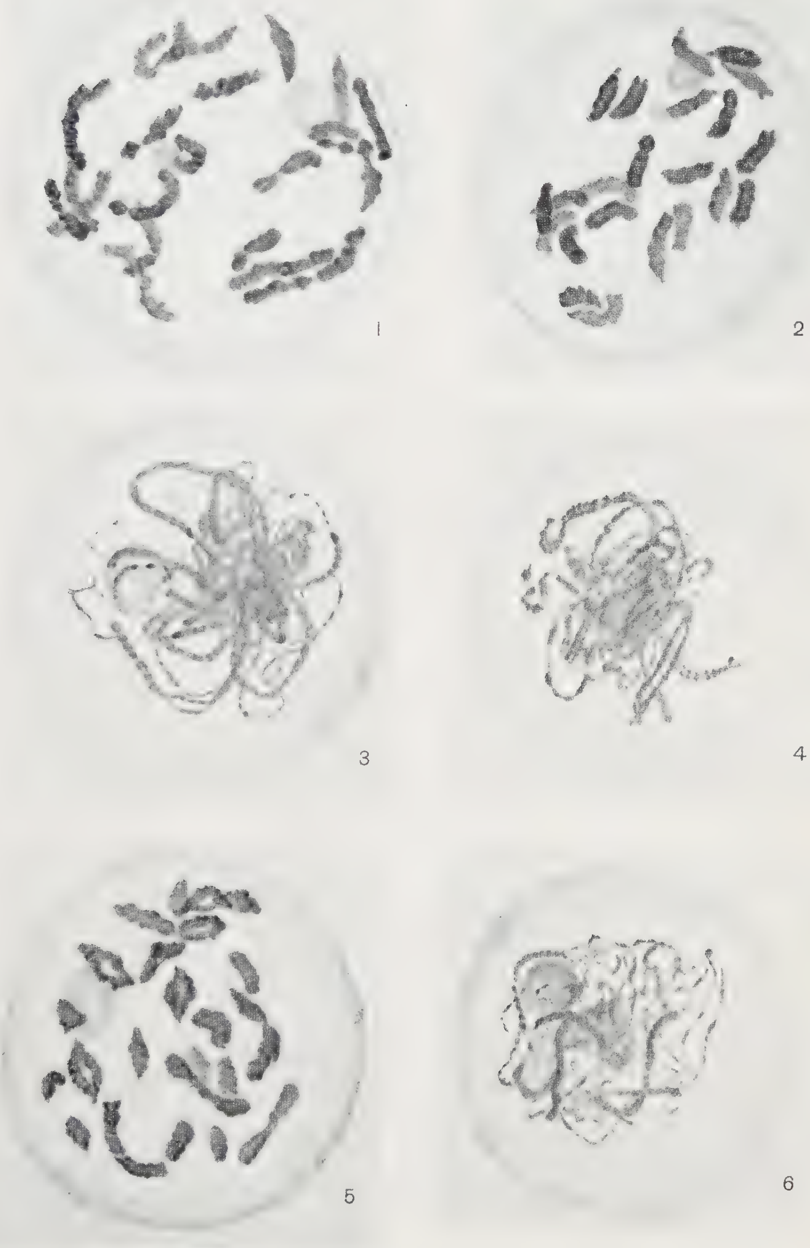
Meiotic prophase of F_1 *Nicotiana glauca* (n = 12) × *N. plumbaginifolia* (n = 10).

FIG. 1. Pre-pachytene. FIG. 2. Pachytene: several short segments associated, unpaired chromosomes exhibiting thick and thin areas. FIG. 3. Later pachytene: distinctions between thick and thin areas more striking; note spiralization in paired segment on extreme right. FIG. 4. Late "pachytene" or early "diplotene": thick and thin areas and spiralization conspicuous. FIG. 5. "Diplotene": chromatid separation apparent. FIG. 6. Diplotene: one paired segment (lower right) possibly with chiasma.

Meiotic Prophase Phenomena in Nicotiana



Meiotic Prophase Phenomena in Nicotiana



Meiotic Prophase Phenomena in Nicotiana

PLATE III

Meiotic prophase of F_1 interspecific hybrids: Figs. 1 and 2 F_1 *N. glauca* × *N. plumbaginifolia*, figs. 3 to 5 F_1 *N. tabacum* (n = 24) × *N. otophora* (n = 12), fig. 6 asynaptic *N. tomentosa* (n = 12).

FIG. 1. Early diakinesis: duality, spiralization, and centromeric position conspicuous. FIG. 2. Diakinesis: secondary association. FIG. 3. Pachytene: paired segments or whole chromosomes and unpaired chromosomes in approximately equal numbers; note thick and thin areas in unpaired lengths. FIG. 4. Diplotene: chiasmata shown in segments of at least three pairs; note identity of spiralization patterns at lower right. FIG. 5. Diakinesis: $12_{II} + 12_{I}$; note evidence of spiralization. FIG. 6. Pachytene: paired segments or whole chromosomes, unpaired segments showing thick and thin areas.

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LA PROTECTION DE LA NATURE A MADAGASCAR

HENRI HUMBERT

Avec cinq planches et une carte

MADAGASCAR est l'une des parties du monde où se révèlent le mieux l'importance des questions relatives à la Protection de la Nature, l'ampleur des problèmes que celle-ci soulève, et les difficultés auxquelles elle se heurte. C'est en même temps, dans l'ensemble des territoires de la France d'Outre-mer, celui où l'effort le plus actif a été entrepris pour la sauvegarde de la flore et de la faune, dont la richesse en espèces endémiques est extraordinaire. Cette richesse, la grande île, fragment du vieux continent de Gondwana, la doit à un long passé géologique au cours duquel des connexions territoriales ont permis, à plusieurs reprises, au cours de l'ère secondaire et de l'ère tertiaire, des migrations floristiques et faunistiques à la faveur desquelles se sont superposés des éléments d'origines diverses, conservés ensuite grâce à l'isolement de cette vaste terre qui couvre environ 600,000 km.[2] Un ensemble de preuves d'ordre principalement biogéographique conduit à placer au Miocène supérieur la dernière de ces connexions.

D'autre part, l'île offre toute une gamme de climats, conditionnés principalement par la disposition des reliefs qui font obstacle aux vents chargés d'humidité soufflant de l'Océan Indien pendant toute la saison fraîche (alizé de S-E.). Le versant oriental ne comporte pas de saison sèche bien marquée et le total annuel de pluies y est élevé (3 mètres et plus dans le N-E.). Sur les hauts plateaux et les montagnes qui les surmontent, parmi lesquelles plusieurs massifs dépassent largement 2,000 m. d'altitude (Tsaratanana, dans le Nord, culminant à 2,886 m.; Ankaratra, dans le Centre, 2,644 m.; Andringitra, dans le Sud-Est, 2,650 m.), la saison fraîche est entrecoupée de fines pluies et le degré hygrométrique est habituellement élevé. L'Ouest au contraire offre deux saisons fortement contrastées: la saison sèche y dure les six mois pendant lesquels l'alizé de S-E., s'étant déchargé de son humidité sur les hauts reliefs, s'échauffe en descendant vers les plaines occidentales; celles-ci reçoivent, par contre, en saison chaude, comme les hauts plateaux et les montagnes du Centre, des pluies orageuses abondantes dans leur partie Nord, de moins en moins copieuses en descendant vers le Sud. Dans le Nord-Ouest, le petit bassin du Sambirano jouit d'un climat spécial, très régulier, chaud et humide, sans saison sèche accusée, comme celui de l'Est, grâce aux reliefs élevés qui relaient en saison fraîche les vents humides de S-E. jusque sur la côte du canal de Mozambique et la petite île de Nossi-be. Le Sud-Ouest et l'extrême Sud sont des pays semi-arides (0 m. 40 à 0 m. 50 de pluies annuelles, sous forme d'averses irrégulières).

Les sols sont eux-mêmes variés, en raison à la fois de la structure géologique et de l'influence des climats sur la décomposition des roches-mères. Ces dernières sont principalement des roches cristallines, éruptives, métamorphiques ou volcaniques, se décomposant sous les climats humides (Est, Centre et Sambirano) en argiles latéritiques d'autant plus épaisses (plusieurs mètres, parfois 10 à 30 mètres) que le climat local est plus constamment pluvieux. Dans la plus grande partie de l'Ouest et dans une partie importante du Sud, se présentent des roches sédimentaires d'origine marine (du Permien au Tertiaire): schistes, grès, sables, calcaires, marnes, argiles, etc.

Les grandes aires de végétation se répartissent, comme toujours, en fonction des caractéristiques climatiques, et, à cet égard, l'île se subdivise en deux Régions. La *Région orientale* comprend l'ensemble des territoires soumis en saison fraîche à l'influence directe de l'alizé humide; elle se subdivise en trois Domaines: *Domaine de l'Est*, depuis le littoral oriental jusqu'aux environs de 800 m. d'altitude; *Domaine du Centre,* au-dessus de 800 m.: *Domaine du Sambirano*, au-dessous de 800 m. dans le bassin du fleuve de ce nom. La *Région occidentale* se subdivise en deux Domaines: *Domaine de l'Ouest et de l'extrême Nord,* au-dessous de 800 m. d'alt. jusqu'au littoral; *Domaine du Sud-Ouest*, suivant une bande de territoire peu profonde le long du littoral Sud-Ouest et Sud.

La composition de la flore et les aspects de la végétation diffèrent considérablement de l'une à l'autre de ces aires, si l'on considère la flore et la végétation *autochtones*. Celles-ci ont été détruites sur d'immenses surfaces par les indigènes, comme nous l'expliquons plus loin, et la végétation secondaire substituée à la végétation primitive contraste violemment avec celle-ci par la pauvreté de sa flore et la monotonie de ses aspects.

La végétation primitive, dans le *Domaine de l'Est et dans celui du Sambirano*, est essentiellement constituée par une haute forêt dense à feuillage persistant, forêt ombrophile (rain-forest) d'une extrême complexité, où les essences sont tellement intriquées qu'il n'y a pas d'espèces nettement dominantes. Les indigènes, d'origine mélanésienne, dont la présence à Madagascar ne remonte pas loin dans le passé (quelques millénaires) se sont attaqués à la forêt orientale par la hache et par le feu (abatage suivi d'incinération) en important la culture du "riz de montagne" et de quelques autres plantes vivrières (manioc, patate douce, bananier, etc.) suivant la méthode dite des "tavy" (semblable à celle des "rây" en Indochine), culture sans irrigation et par suite nécessairement extensive, en raison de l'épuisement rapide du sol. Ils ont déforesté à partir de la côte et, de proche en proche, le long des vallées et vallons les plus accessibles des pentes orientales qui s'élèvent à peu de distance de celle-ci, de sorte que c'est généralement vers le haut des mamelons et sur les versants escarpés que subsistent encore des restes de forêts plus ou moins étendues, dans ce domaine. Sous le climat habituellement humide qui le caractérise, une végétation secondaire envahissante se développe après la destruction de la forêt; les indigènes lui donnent le nom de "savoka"

qui s'applique à divers types de peuplements, composés d'arbustes ou petits arbres ou encore de grandes monocotylédones herbacées, essences de lumière occupant solidement le terrain et formant une sorte de jungle qui pourrait, dans les conditions les plus favorables, faire retour à la forêt si l'homme n'intervenait pas de nouveau et s'il restait des parcelles boisées au voisinage. Mais, en fait, les savoka, dont le sol se dégrade facilement sur les pentes, sont à leur tour attaqués de temps en temps par les incendies et en règle générale c'est une évolution régressive que l'on constate: le savoka cède peu à peu le pas à des formations graminéennes et celles-ci transmettent aisément les incendies quand les chaumes sont secs; même sous le climat habituellement humide de l'Est, la prairie secondaire occupe une grande partie du terrain abandonné par la forêt d'abord et par les savoka ensuite. Il en est de même dans le domaine du Sambirano.

Dans le *Domaine du Centre*, les savoka occupent de bien moindres étendues; ils se présentent le plus souvent sous forme de peuplements buissonnants constitués en majeure partie d'Ericacées du genre *Philippia* accompagnées d'autres espèces héliophiles qui vivent normalement dans la végétation primitive sur les crêtes et les escarpements ou dans les ravins interrompant le couvert continu de la forêt dense; ils se rencontrent surtout dans la partie orientale plus humide de ce domaine, ceinturant les lisières forestières en régression ou occupant l'emplacement de forêts récemment détruites. Les savoka de ce type brûlent facilement et à leur tour sont remplacés par la prairie secondaire d'herbes dures (*Aristida*, etc.) qui s'étend maintenant sur la presque totalité de ce domaine, où il devient très difficile de trouver encore des témoins de la forêt native, sauf sur quelques montagnes ou plateaux protégés par des escarpements ayant fait pare-feux. L'immense étendue de cette prairie du Centre a fait croire autrefois que c'était une steppe climatique. C'est là une grosse erreur aujourd'hui reconnue par tous les botanistes et les forestiers qui ont suivi son évolution: ce n'est qu'un "fire-climax"; les incendies y sont allumés chaque année par les indigènes pour provoquer le départ des jeunes feuilles de graminées en vue de la nourriture du bétail en saison sèche; mais ce procédé élimine peu à peu les espèces bonnes fourragères au profit des espèces les plus xérophiles et finit par ruiner les pâturages, dont le sol se décape et se durcit de plus en plus: l'argile latéritique mise à nu apparaît et donne au paysage cette teinte rouge ou ocre devenue caractéristique de ces contrées aujourd'hui presque entièrement dépouillées de leur couvert végétal primitif.

Celui-ci était constitué par une forêt toujours verte, moins puissante que celle de l'Est, très riche en épiphytes, à sous-bois formé d'espèces mésophiles à feuillage tendre avec une abondance remarquable de Muscinées, le passage de l'une à l'autre étant d'ailleurs trés ménagé. Mais sur les pentes occidentales de ce Domaine, plus sèches et plus lumineuses, où règne un climat de transition vers le climat de l'Ouest, c'était une forêt basse et claire très différente, formée de petits arbres sclérophylles, avec un riche sous-bois relativement xérophile et héliophile; facilement inflammable, elle a presque entièrement disparu. D'autre part, en altitude, à partir de

2.000 m. environ, la forêt du Centre passait à une végétation dense d'arbres tortueux et bas surchargés de Lichens épiphytes pendant aux branches et de Muscinées garnissant les troncs: cet étage forestier supérieur correspond au niveau le plus nébuleux et le plus humide des montagnes. Plus haut, il passe à des formations buissonnantes très riches en espéces spéciales, formant une sorte de maquis dense, difficilement pénétrable sauf sur les rochers escarpés où habitent de très nombreuses plantes basses particulières à ce genre de station. Chaque massif de montagnes possède des espèces qui lui sont propres, à aire par conséquent très réduite, en même temps que des espèces à aire fragmentée communes à l'ensemble ou à une portion des hauts reliefs.

Cette végétation des sommets ne craint pas la foudre, qui coïncide avec les grandes pluies, mais elle est très sensible aux incendies venus de la nappe graminéenne secondaire, lorsque celle-ci arrive à son contact après la fragmentation de la ceinture forestière de l'étage immédiatement inférieur. Aussi voit-on souvent des restes de cette dernière dans les vallonnements plus frais, où ils se maintiennent plus longtemps, ou au flanc des pentes, alors que les croupes des contreforts et les crêtes supérieures sont déjà dénudées et occupées par la prairie, si des obstacles rocheux n'ont pas arrêté les feux: l'aspect de ces juxtapositions est bien différent de celui qui s'offre dans l'Est. La prairie se substitue presque immédiatement à la forêt, sauf dans la partie orientale de ce domaine: les feux atteignent directement ses lisières et les font régresser lentement mais inexorablement; les formations éricoïdes des sommets peuvent même brûler en masse, par temps sec, lorsque le vent y pousse les flammes.

La végétation autochtone du *Domaine de l'Ouest et de l'extrême Nord* était constituée par des forêts variées composées d'essences à feuillage généralement caduc. Il en reste encore d'importantes étendues, principalement sur les plateaux calcaires et les sols sablonneux. Certaines d'entre elles, à basse altitude, offrent de splendides exemples de forêt tropophile (deciduous forest) de haute futaie. Dans ce Domaine, où les affleurements géologiques sont très variés, on peut constater de grandes différences de composition floristique et d'aspect dans les formations forestières primitives, en rapport avec la nature du sol: il y a là, sous un même climat, des "climax édaphiques" nettement différents.

La destruction de ces forêts, par "tavy" ou par "feux de brousse" venus de l'extérieur, amène l'extension de formations secondaires graminéennes souvent piquetées d'arbres ou d'arbustes appartenant à quelques espèces résistant aux feux, à racines profondes ou drageonnantes; parmi ces espèces, certaines ont un port caractéristique, tels quelques Palmiers des genres *Medemia, Hyphaene* et *Borassus*. Aussi ce domaine offre-t-il divers aspects de savanes, arborées ou non, que les feux parcourent annuellement; ceux-ci pénètrent parfois assez profondément dans l'intérieur du complexe forestier et en provoquent le recul. Sur les sols argileux ou marneux, et en général sur ceux où la prairie secondaire, haute et dense, alimente les incendies les plus violents, les végétaux ligneux sont souvent totalement éliminés.

Le *Domaine du Sud-Ouest*, le plus sec de l'île, est celui qui a conservé les plus grandes étendues de végétation intacte, parceque celle-ci, formée de petits arbres et arbustes en partie succulents (notamment de nombreuses Euphorbes arborescentes), brûle difficilement, à moins d'être abattue; mais comme, sous ce climat, les cultures ne sont guère possibles que sur des sols alluviaux riches, les "tavy" ne sont que rarement pratiqués. Les formations graminéennes, sur sols habituellement rocailleux ou sablonneux, sont maigres, les feux sont par conséquent peu puissants et s'arrêtent aux lisières du complexe végétal primitif.

La destruction généralisée du couvert végétal à Madagascar a eu d'immenses conséquences: décapage des terres meubles, qui entraînées par les grandes pluies de la saison chaude viennent finalement se perdre en grande partie à la mer qu'elles rougissent jusqu'à plusieurs milles de l'embouchure des fleuves; ravinement des pentes, instauration d'un nouveau cycle d'érosion aux contours heurtés, aggravation du régime torrentiel avec ses suites désastreuses. Tels sont les résultats des méthodes pratiquées par l'indigène pour étendre sans effort cultures et pâturages par l'usage généralisé des incendies qui parcourent la majeure partie de l'île pendant la saison sèche.

On conçoit dès lors quelles difficultés se présentent aux promoteurs d'une oeuvre de protection de la nature destinée à sauver pendant qu'il en est encore temps des surfaces aussi importantes et diverses que possible de la merveilleuse végétation native, tant dans un but scientifique de conservation des innombrables espèces végétales et animales constituant les "biocénoses" primitives, que dans un but économique.

Le but scientifique a été plus spécialement visé par l'adoption de la formule des "Réserves naturelles intégrales" dont la définition a été proposée par les délégués français à la conférence internationale pour la Protection de la Faune et de la Flore en Afrique réunie à Londres en 1933. Cette définition, différente de celle des "Parcs Nationaux" adoptée à la même Conférence, est la suivante:

Réserves naturelles intégrales. — "L'expression *Réserve Naturelle intégrale* désignera une aire placée sous le contrôle public et sur toute l'étendue de laquelle toute espèce de chasse ou de pêche, toute exploitation forestière, agricole ou minière, toutes fouilles ou prospections, sondages, terrassements ou constructions, tous travaux tendant à modifier l'aspect du terrain ou de la végétation, tout acte de nature à nuire ou à apporter des perturbations à la faune ou à la flore, toute introduction d'espèces zoologiques ou botaniques, soit indigènes, soit importées, sauvages ou domestiquées, seront strictement interdits; où il sera défendu de pénétrer, de circuler, ou de camper sans autorisation spéciale écrite des autorités compétentes; et dans laquelle les recherches scientifiques ne pourront être effectuées qu'avec la permission de ces autorités."[1]

[1] Voici, à titre de comparaison, la définition des Parcs Nationaux telle que l'a établie cette même Conférence.

Parcs Nationaux. — "L'expression *Parc National* désignera une aire placée sous le

Dès 1927, un décret du 31 décembre paru au Journal Officiel de la République Française avait institué à Madagascar 10 Réserves naturelles intégrales distribuées dans chacun des Domaines définis plus haut et aux divers étages altitudinaux; une onzième fut créée par décret du 11 juin 1939. En voici l'énumération avec le no. de la réserve, la province où elle est située, la surface, et le type de végétation qu'elle représente:

RÉSERVES NATURELLES INTÉGRALES DE MADAGASCAR

R.N.No. 1 — Betampona (province de Tamatave), 1,632 hectares. — Forêt ombrophile.

R.N.No. 2 — Cap Masoala (province de Maroantsetsa), 29,977 hect. — Forêt ombrophile.

R.N.No. 3 — Zakamena (province de Moramanga), 66,410 hect. — Forêt ombrophile.

R.N.No. 4 — Tsaratanana (province de Nossi-bé), 59,280 hect. — Forêt ombrophile et étages supérieurs de végétation.

R.N.No. 5 — Andringitra (province de Fianarantsoa), 30,100 hect. — Forêt ombrophile et étages supérieurs de végétation.

R.N.No. 6 — Lokobe (province de Nossi-bé), 1,160 hect. — Forêt ombrophile à basse altitude.

R.N.No. 7 — Ankarafantsy (province de Majunga), 67,000 hect. — Forêt tropophile sur sables siliceux.

R.N.No. 8 — Tsingy de Namoroka (province de Majunga), 5,900 hect. — Forêt tropophile sur calcaire.

R.N.No. 9 — Tsingy de Bemaraha ou Antsingy (province de Maintirano), 83,600 hect. — Forêt tropophile sur calcaire.

R.N.No. 10 — Bush du plateau Mahafaly et lac Manampetsa (province de Tuléar), 17,520 hect. — Bush xérophile sur calcaire et sables.

R.N.No. 11 — Massif d'Andohahela ou Rocher Carré (province de Fort-Dauphin), 30,000 hect. — Divers étages de végétation, de 300 à 1,975 m. alt.; versant oriental et versant occidental très contrastés: forêts ombrophiles, végétation buissonnante des crêtes, forêts tropophiles, bush xérophile, etc.

contrôle public, dont les limites ne seront pas changées et dont aucune partie ne sera capable d'être transférée sauf par l'autorité législative compétente, mise à part pour la propagation, la protection et la conservation de la vie animale sauvage et de la végétation sauvage, et pour la conservation d'objets d'intérêt esthétique, géologique, préhistorique, historique, archéologique, et d'autres intérêts scientifiques, au profit, à l'avantage et pour la récréation du public général, dans laquelle la chasse, l'abatage ou la capture de la faune et la destruction ou la collection de la flore est interdite sauf par l'entreprise ou sous la direction ou le contrôle des autorités du parc."

Il est à noter que ces deux définitions ne s'excluent pas l'une l'autre, une ou plusieurs Réserves naturelles intégrales pouvant être incluses dans un Parc National.

Les divers types de végétation sont représentés de la façon suivante:
Domaine de l'Est: Réserves naturelles intégrales nos. 1, 2, 3 (partie), 11 (partie).
Domaine de Sambirano: R.N.I. no. 6.
Domaine du Centre: R.N.I. no. 3 (partie), 4, 5, 11 (partie).
Domaine de l'Ouest: R.N.I. nos. 7, 8, 9, 11 (partie).
Domaine du Sud-Ouest: R.N.I. nos. 10, 11 (partie).

Ces Réserves sont gérées et surveillées par un service spécial rattaché à celui des Forêts et à la tête duquel se trouve un Officier forestier, conservateur des Réserves naturelles. Elles ont été délimitées et immatriculées au nom de l'Etat français. Leurs limites ont été choisies autant que possible en suivant des lignes de protection naturelle (cours d'eau, escarpements,

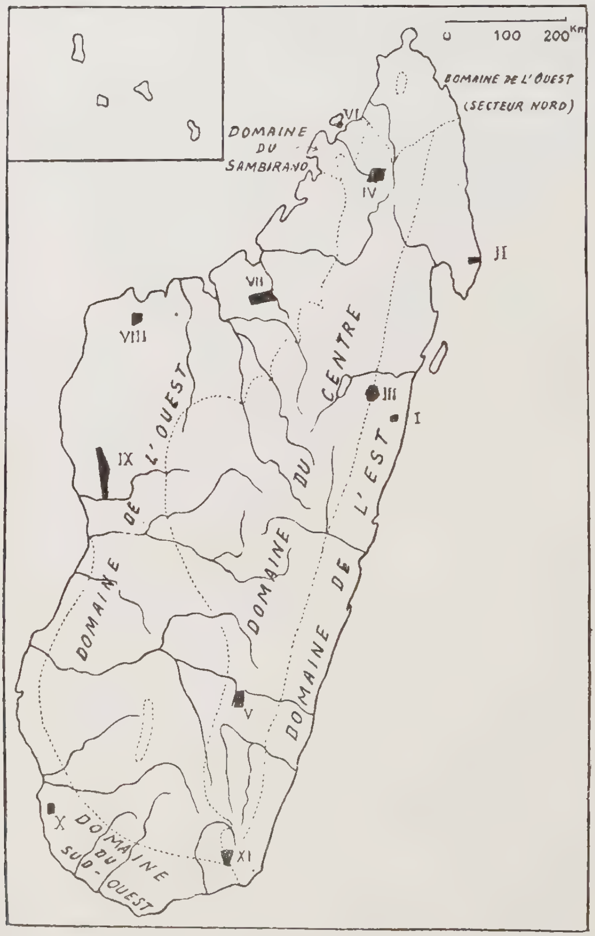

FIG. 1. Réserves naturelles intégrales de Madagascar. Les limites des Domaines de Végétation sont indiquées par le pointillé.

etc.) et, partout où il est nécessaire, des lignes de protection artificielle contre les feux de brousse (pare-feux, etc.) ont été prévues, et établies par ordre d'urgence. Des zones intermédiaires de protection (périmètres de reboisement, etc.) ont été ménagées sur certaines parties de leurs pourtours. Leur bornage, jalonnant des pistes qui matérialisent leurs limites, a été également entrepris, mais la guerre a interrompu ces travaux. Ces Réserves naturelles intégrales, choisies dans des territoires inhabités, représentent la nature primitive intacte.

Il est à peine besoin d'indiquer ici que la prééminence donnée au but scientifique dans la conception de ces Réserves naturelles intégrales n'exclut aucunement l'intérêt d'ordre économique, bien au contraire. Elles sont en effet destinées à la conservation, dans leur milieu naturel, des milliers d'espèces propres à Madagascar, et il n'est pas douteux qu'un grand nombre de ces espèces est susceptible d'utilisations de tout ordre. Elles constituent donc les plus précieuses réserves de porte-graines qu'il soit possible de conserver en vue de futures cultures, ou de reboisements, etc. Mais, et c'est là une différence capitale avec les Réserves forestières ordinaires, elles ne sont pas des Réserves d'exploitation. Par ailleurs, elles permettront les observations les plus fructueuses sur l'évolution naturelle des peuplements végétaux autochtones. Enfin elles protègent contre l'érosion et ses conséquences des surfaces importantes de territoires dont plusieurs sont des massifs montagneux dont la déforestation totale serait désastreuse par les répercussions qu'elle aurait sur le régime des eaux et même sur le climat des contrées environnantes.

Récemment, deux décrets parus au Journal Officiel de la République Française (1945, no. 143) fixent les conditions de réglementation de la protection de la nature dans les territoires relevant du Ministère des Colonies (décret no. 45–1344 du 18 juin 1945) et instituent un Conseil Supérieur de la Protection de la Nature aux Colonies (décret no. 45–1347, même date), qui remplace un Comité préexistant.

D'autre part, un grand nombre de stations naturelles est soumis également à une protection spéciale instaurée par le décret du 25 août 1937 relatif à la Protection des monuments naturels et des sites de caractère historique, scientifique, légendaire ou pittoresque des colonies, pays de protectorat et territoires sous mandat relevant du Ministère des Colonies. Sous cette désignation sont compris notamment d'intéressants témoins de végétation native, qui pour diverses raisons (généralement leur faible étendue) ne pouvaient constituer des Réserves naturelles intégrales. Des grottes, des gisements fossilifères, etc. sont aussi visés par ce texte.

Il n' a pas été créé jusqu'ici à Madagascar de Parcs nationaux ouverts au tourisme, mais cette création n'est nullement exclue: par exemple, la belle forêt de la montagne d'Ambre près de Diégo-Suarez, déjà pourvue de routes, offrant de très beaux sites (cratères-lacs), s'y prête parfaitement.

Quant à l'ensemble du domaine forestier, au sens le plus large, en dehors des territoires spécialement protégés suivant les formules précédentes, il est soumis au contrôle du service des Forêts. Le régime des "tavy" et les

exploitations abusives sont interdits, mais, en fait, les tavy sont encore trop souvent pratiqués clandestinement dans les territoires d'accès difficile où la surveillance est sporadique.

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EXPLICATION DES PLANCHES

PLANCHE I

En haut: Forêt ombrophile. Vallée de la Rienana, vers 1,000 m. alt. (H. H., 1924).

En bas: Forêt ombrophile. Massif du Beampingaratra, vers 1,000–1,400 m. alt. (H. H., 1928).

PLANCHE II

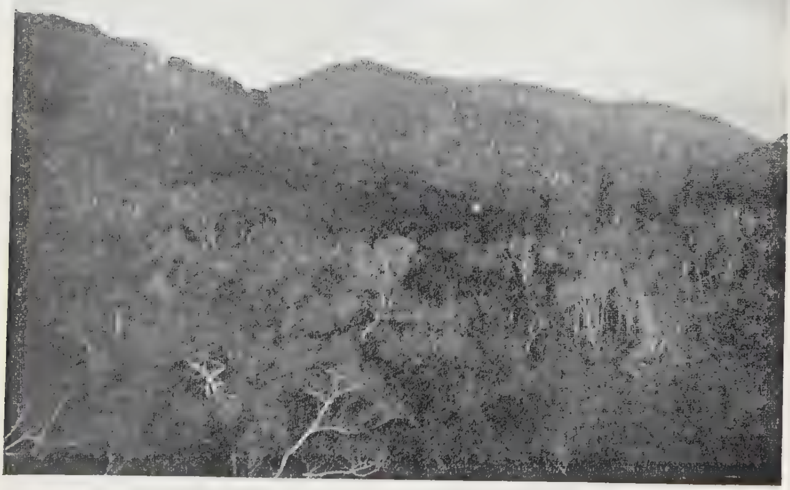
En haut: Forêt des crêtes. Massif du Kalambatitra, sommet de Beanjavidy, vers 1,700 m. alt. (H. H., 1933).

En bas: Végétation éricoïde des sommets: *Philippia* arborescents couverts d'épiphytes. Massif du Tsaratanana, vers 2,750 m. alt. (H. H., 1937).

PLANCHE III

En haut: Forêt basse sclérophylle des pentes occidentales, vers 1,000 m. alt. Vallée de la Manambolo, affluent du Mandrare. (H. H., 1934).

En bas: Forêt tropophile de haute futaie à basse altitude, dans l'Ouest. Environs de Morondava. En avant *Adansonia Za* Baill. (en saison sèche) (H. H., 1933).



La Protection de la Nature à Madagascar

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PLANCHE IV

En haut: Forêt xérophile, faciès de transition entre la forêt de l'Ouest et le bush de l'extrême Sud, vers 200 m. alt. Vallée moyenne du Mandrare, *Adansonia Za* Baill. (en saison des pluies), *Alluaudia procera* Drake (arbre céréiforme) (H. H., 1933).

En bas: Bush xérophile sur le plateau calcaire Mahafaly, vers 150 m. alt. Euphorbes arborescents de la section *Tirucalli*, etc. (H. H., 1928).

PLANCHE V

En haut: Prairie secondaire du Centre substituée par le régime des feux à la forêt du type représenté pl. 1, en bas. Haut Itomampy. (H. H., 1928).

En bas: Savane secondaire à *Hyphaene Schatan* Boj. substituée par le régime des feux à la forêt tropophile de l'Ouest. Environs d'Ambilobé (secteur Nord) (H. H., 1937).

MUSÉUM NATIONAL D'HISTOIRE NATURELLE,
PARIS.

A REPORT ON THE GROWTH OF EXCISED TOMATO ROOTS

WILLIAM J. ROBBINS

With one plate

IT WAS found by Robbins and Schmidt (5, 6, 7) that a solution of mineral salts, cane sugar and thiamine (or the vitamin thiazole, 4-methyl-5β-hydroxyethyl thiazole) appeared adequate for the unlimited growth of excised tomato roots. The first report (5, 7) covered 12 successive passages extending over a period of one year in a solution of mineral salts, cane sugar and synthetic thiamine and seven successive passages in a period of seven months in the same solution with thiazole substituted for thiamine. The second report (10) was made at the end of 29 passages in the thiamine solutions and 23 in those containing thiazole. We have now maintained this strain of roots through 125 passages for a period of ten years and ten months since the roots were severed from the original seedlings on September 29, 1935. The clones have been grown for 112 successive passages in a solution of mineral salts, cane sugar and thiamine and for 105 successive passages in a solution of mineral salts, cane sugar and thiazole.

These experiments are of interest because of the extended period of culture. Some additional observations have been made on this strain of roots, which are also recorded here.

CONDITIONS OF CULTURE

The excised roots were grown individually in 50 ml. of solution in 125 ml. Erlenmeyer flasks of Pyrex glass. The mineral salts were of C. P. grade; the cane sugar, Pfanstiehl's C. P. sucrose; the thiamine, Merck's synthetic. The 4-methyl-5β-hydroxyethyl thiazole was obtained through the courtesy of Merck & Co. It was free from vitamin pyrimidine as determined by tests with *Phycomyces blakesleeanus*. This is an important consideration, as we have had samples of thiazole contaminated with pyrimidine and others have reported to us similar difficulties. All glassware was cleaned with sulfuric-chromic acid cleaning mixture and thoroughly rinsed with tap and distilled water. A comparison of the growth of excised tomato roots in glassware cleaned with sulfuric-chromic acid cleaning mixture and in glassware cleaned with concentrated hydrochloric acid showed no differences. We concluded that the residual effects of chromium (3) were not important in these experiments.

For the last several years the roots have been cultivated in a modified Pfeffer's solution plus one per cent cane sugar and 10 mμ moles of thiamine or of thiazole per flask. The modified Pfeffer's solution was prepared

by diluting stock solutions of the various salts. Our procedure was as follows: The stock solutions consisted of

I.	$Ca(NO_3)_2.4\ H_2O$	83.25 g.
	$Fe_2(SO_4)_3$	0.565 g.
	Distilled water	500 ml.
II.	KCl	20.8 g.
	KNO_3	41.6 g.
	KH_2PO_4	41.6 g.
	$MgSO_4.7H_2O$	41.6 g.
	Distilled water	500 ml.
III.	H_3BO_3	2.86 g.
	$MnSO_4.4H_2O$	2.04 g.
	or	
	$MnCl_2.4H_2O$	1.81 g.
	$ZnSO_4.7H_2O$	0.22 g.
	$CuSO_4.5H_2O$	0.08 g.
	$H_2MoO_4.H_2O$	0.09 g.
	Distilled water	1000 ml.

Two ml. of stock solution I, 1 ml. of II and 0.1 ml. of III were added to 1000 ml. of distilled water.

The final solution contained per liter 333 mg. $Ca(NO_3)_2{\cdot}4H_2O$, 41.6 mg. KCl. 83.2 mg. KNO_3, 83.2 mg. KH_2PO_4, 83.2 mg. $MgSO_4{\cdot}7H_2O$, 2.26 mg. $Fe_2(SO_4)_3$, 0.286 mg. H_3BO_3, 0.181 mg. $MnCl_2{\cdot}4H_2O$, 0.022 mg. $ZnSO_4{\cdot}7H_2O$, 0.008 mg. $CuSO_4{\cdot}5H_2O$, 0.009 mg. $H_2MoO_4{\cdot}H_2O$. The approximate amounts of the supplemental mineral elements in parts per million in this solution were 0.32 Fe, 0.05 B, 0.05 Mn, 0.005 Zn, 0.002 Cu and 0.005 Mo.

The iron precipitated in stock solution I but by shaking satisfactory aliquots could be obtained. The other stock solutions remained clear and without precipitate.

The amount of sugar was found to be quite important. One per cent sugar was much superior to the two per cent used in the early passages (Pl. I, upper). The growth of replicate cultures was more uniform; the individual roots were more normal in appearance and showed less browning.

The modified Pfeffer's solution containing cane sugar can be autoclaved at 12 pounds pressure for 20 minutes with no deleterious effects as far as the growth of the tomato roots is concerned and with minor inversion of the cane sugar.

Transfers to fresh culture media were made at approximately monthly intervals. A portion, about 0.5 cm. square of a safety razor blade spot-welded on an iron wire held in a Rosenberger and Greenman needle holder was used to cut the roots into pieces. The pieces of root were one or two cm. long and included the primary root tip or one or more branch tips. The pieces were transferred to fresh culture media by a platinum wire bent into an L at the tip. This was found to be more convenient than a straight wire or one with a loop on the end.

For some years the roots were incubated in faint diffuse light at 25°C. Since the incubator was not equipped to run at temperatures below room temperature there were periods during the summer months when the incubator temperature exceeded 25°, rising to as much as 30° for part of some days. Some difficulty was experienced at times in maintaining the thiazole cultures. This we suspect may have been caused by the higher temperatures of the summer months. Our cultures are now being maintained at 20° in the dark. They are exposed to light occasionally for short periods when observations are made.

Growth has been measured by dry weights usually at the end of two months' growth. The roots were washed with distilled water, placed in weighed aluminum pans, dried at 100°C., cooled and weighed. The results for passages 84 to 96 inclusive are given in TABLE 1. The average

TABLE 1.

Growth of excised tomato roots in modified Pfeffer's solution, 1 per cent cane sugar and 10 mμ moles of thiamine or thiazole through 13 successive passages.

Date	Passage	Supplement	No. Roots Weighed	Dry Wt. per root mg.	Range Dry Wt. mg.
10/7/42 to	84	Thiamine	20	6.5	4.9– 9.8
12/10/42		Thiazole	5	7.8	5.1–10.0
11/9/42 to	85	Thiamine	18	9.5	6.2–15.2
1/8/43		Thiazole	23	5.7	1.5–10.4
....	86	No weights taken			
1/12/43 to	87	Thiamine	49	10.5	5.0–16.1
3/24/43		Thiazole	31	6.0	1.0–11.7
2/11/43 to	88	Thiamine	3	8.6	6.0–13.4
4/16/43		Thiazole	12	5.6	2.3– 8.7
3/12/43 to	89	Thiamine	6	9.8	8.1–12.3
5/13/43		Thiazole	23	7.7	4.6–10.7
4/13/43 to	90	Thiamine	19	9.4	6.8–12.0
6/12/43		Thiazole	25	9.9	0.9–15.1
5/11/43 to	91	Thiamine	2	9.8	....
7/19/43		Thiazole	23	12.0	....
6/10/43 to	92	Thiamine	24	7.8	....
8/10/43		Thiazole	24	12.9	....
7/6/43 to	93	Thiamine	3	8.8	....
9/9/43		Thiazole	22	13.8	....
8/4/43 to	94	Thiamine	14	13.8	....
10/11/43		Thiazole	25	13.2	....
9/6/43 to	95	Thiamine	21	9.2	....
11/9/43		Thiazole	12	16.2	....
10/6/43 to	96	Thiamine	23	13.4	....
12/10/43		Thiazole	24	8.8	....

dry weights of the roots varied somewhat from passage to passage. In the 12 passages given the lowest average dry weight in the thiamine solutions was 6.5 mg. and the highest 13.3 mg.; for the thiazole solutions these figures were 5.6 mg. and 16.2 mg.

RELATION TO VITAMINS

Robbins and Schmidt demonstrated by the use of *Phycomyces blakesleeanus* that this strain of tomato roots synthesizes the pyrimidine portion of thiamine or a substitute therefor. This accounts for the ability of these roots to grow indefinitely in a medium supplemented with the vitamin thiazole only.

Reid and Robbins (2) found the excised roots grown in a thiamine solution produced ascorbic acid.

I have found the roots to synthesize biotin and pyridoxine in solutions supplemented with thiamine or thiazole. This was demonstrated as follows:

Roots which had grown 57 days in the thiamine solution in passage 73 were immersed in a medium containing per liter 1.5 g. KH_2PO_4, 0.5 g. $MgSO_4 \cdot 7H_2O$, 50 g. dextrose, 2.0 g. asparagine and 1.5 per cent purified agar. Zero, one or three roots were added per tube containing 8 ml. of the agar medium. The average dry weight per root was 6.8 mg. After sterilization one set of tubes was inoculated with *Ceratostomella ulmi* and another with *Ceratostomella ips* #438; *C. ulmi* has a complete deficiency for pyridoxine and *C. ips* #438 for biotin (4). The only source of vitamins in the medium was the tomato roots. The growth of *C. ulmi* demonstrated the presence of pyridoxine or a substitute for it and that of *C. ips* #438 the presence of biotin (Pl. I, lower).

A similar experiment performed with roots grown in a thiazole solution showed the synthesis of biotin and pyridoxine in that medium also.

The demonstration that these tomato roots synthesize pyridoxine in a solution of mineral salts, cane sugar and thiamine or thiazole explains their ability to grow in a solution containing no pyridoxine. They require pyridoxine and in its absence from the medium synthesize enough for some growth though not enough for maximum growth.

Our determinations of pyridoxine in excised tomato roots were not quantitative. However, it is reasonable to suppose that the marked improvement in growth noted (8, 9) when pyridoxine is added to the thiamine medium is because the amount of pyridoxine synthesized by the roots is inadequate. In the thiamine solution growth is limited by the amount of pyridoxine synthesized and the addition of the latter vitamin to the medium permits more growth to occur.

Pyridoxine, Pyridoxal and Pyridoxamine. Snell (11) found that pyridoxal and pyridoxamine were as effective for some organisms as pyridoxine and in some instances were considerably more so. For the strain of tomato roots discussed in this paper pyridoxal and pyridoxine were equally effective under the conditions of our experiments. Pyridoxamine may be somewhat less active since as much dry weight was found with 10 mμ moles of the first two compounds as with 50 mμ moles of pyridoxamine. The difference, however, is not great and is not of the same order of magnitude as found by Snell (11) for some organisms, for example, *Lactobacillus casei* and

Streptococcus lactis R. Our excised tomato roots are apparently able to convert these compounds into the functional one whatever that may be.

In the experiments summarized in TABLE 2 the pyridoxal and pyridoxamine were filtered sterile and added to the balance of the solution after it

TABLE 2.

Dry weights of excised tomato roots grown two months in 50 ml. of modified Pfeffer's solution containing one per cent cane sugar, 10 mμ moles of thiamine and the amounts of pyridoxine, pyridoxamine or pyridoxal given in the table.

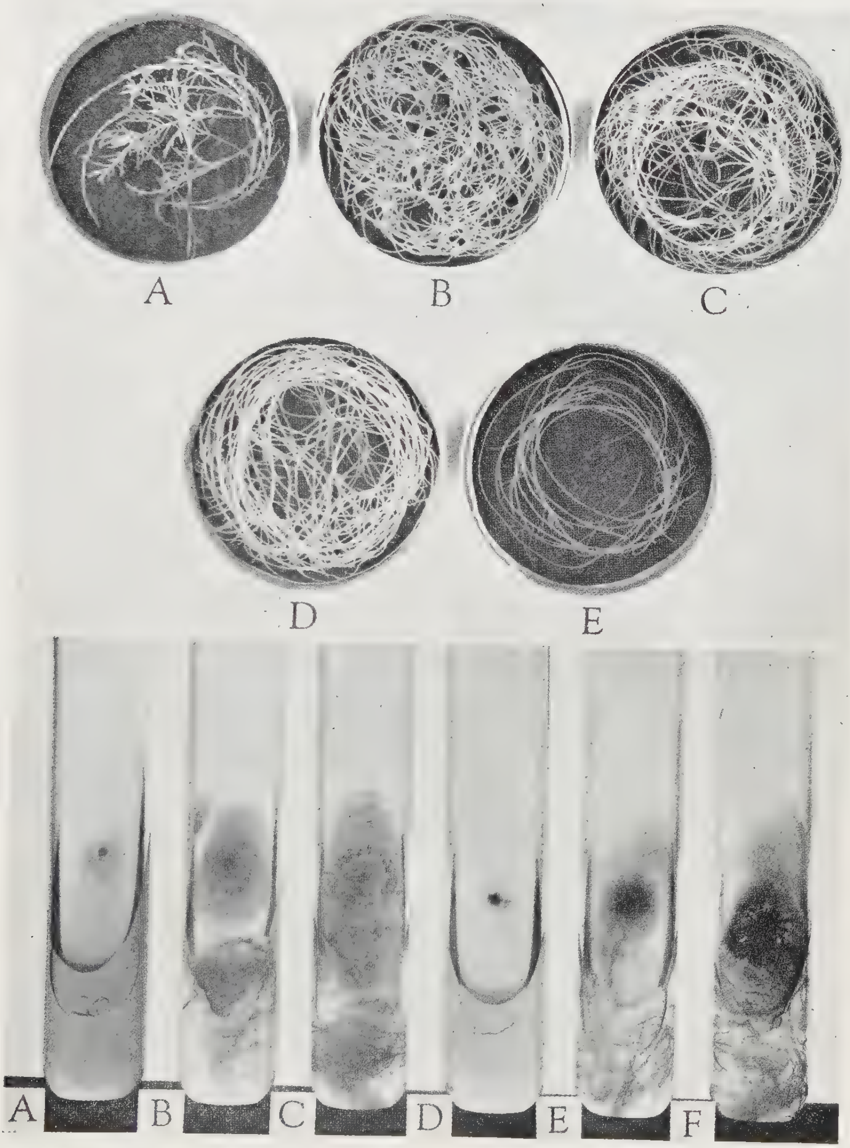
	Pyridoxine			Pyridoxamine			Pyridoxal		
Supplement in mμ moles	No. Roots	Av. dry wt. mg.	Range mg.	No. Roots	Av. dry wt. mg.	Range mg.	No. Roots	Av. dry wt. mg.	Range mg.
100	9	27.2	22.2–29.3	9	27.9	24.9–30.9	10	28.5	26.1–29.8
50	10	24.8	18.4–28.5	9	24.3	19.7–27.3	10	26.0	22.6–29.4
10	9	25.5	21.3–29.7	10	17.1	15.1–19.9	7	24.2	22.6–28.3
1	10	14.5	11.2–20.4	7	12.7	10.7–14.6	9	14.7	12.0–17.1
0.1	8	13.0	11.1–14.5	10	13.5	10.6–16.1	9	15.2	8.4–18.3
0.0	9	14.3	12.4–17.7	9	14.3	12.4–17.7	9	14.3	12.4–17.7

had been autoclaved. The inoculum came from roots grown 24 days in a thiamine solution in passage 107. The roots were incubated in faint diffuse light.

We might expect considerable destruction of these compounds in diffuse light in a period of two months on the basis of the findings of Cunningham and Snell (1). Although it would be desirable to repeat our experiments with roots grown in the dark, we doubt whether our conclusions on the relative effectiveness of the three compounds would be changed. We have been unable to detect a difference in the dry weights of excised tomato roots grown two months side by side in the dark and in the light in solutions containing thiamine or thiamine and pyridoxine.

During this extended period of culture (more than 100 passages) we have observed no evidence that the roots have changed genetically. They appear to be growing now about as they did in 1939 or earlier. Neither has there been any sign of the production of shoots, although we would expect shoot production to be within their genetic potentialities.

We have produced individual roots with dry weights of 200 mg. or more. These were grown 106 days at room temperature in diffuse light in liter flasks containing 100 ml. of the modified Pfeffer's solution and one per cent cane sugar plus 30 mμ moles of thiamine and 166 mμ moles of pyridoxine. In a period of two months in 50 ml. of solution supplemented with 10 mμ moles of thiamine and 50 mμ moles of pyridoxine the maximum



Growth of excised tomato roots

weights range between 35.0 and 40.0 mg. In thiamine-pyridoxine solutions increases in length averaging 2 cm. per day for a period of two months have been observed, resulting in roots with a total length of 120 cm.

SUMMARY

A report is made on the cultivation of excised tomato roots in a synthetic solution of mineral salts, cane sugar and thiamine or thiazole through more than 100 passages extending over nearly eleven years. The cultural conditions are detailed and the relation of the roots to vitamins is discussed.

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EXPLANATION OF THE PLATE

(Upper) Excised roots grown 60 days in diffuse light at 25° in 50 ml. of modified Pfeffer's solution containing 10 mμ moles of thiamine and 50 mμ moles of pyridoxine plus A, 2 per cent cane sugar; B, 1.5 per cent; C, 1.0 per cent; D, 0.5 per cent and E, 0.1 per cent.

(Lower) Growth of *Ceratostomella ulmi* (A, B, C) and *Ceratostomella ips* #438 (D, E, F) in media containing tomato roots. A, no root; B, one tomato root; C, 3 tomato roots; D, no root; E, one root; F, 3 roots.

New York Botanical Garden
and
Department of Botany,
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THE ARNOLD ARBORETUM DURING THE FISCAL YEAR ENDED JUNE 30, 1946

1935 — 1946

THIS is my final report as Director of the Arnold Arboretum. My resignation was presented in June, but too late to be acted upon before the end of the fiscal year.* While I retain my academic title as Arnold Professor of Botany, Harvard University, for the next two years, and will continue to work at the Arboretum, I will have no further administrative responsibilities. As a matter of record I attain the age of 70 in October of the present year, and will become *emeritus* at the end of June, 1948.

Under the reorganization plans as outlined in the Bailey report which was officially approved March 1, 1946, the position of Administrator of Botanical Collections was officially terminated, and I was relieved of all responsibilities effective at the end of June, 1946. The projected reorganization of the very complex botanical situation at Harvard University involves a much closer affiliation of the nine separately endowed units in botany with the Department of Biology of the University, and a closer coördination of their work with that of the Department, both in teaching and in research. The new plan provides for a Biological Council under which will function two chairmen, one in charge of the Institute for Research in General Plant Morphology, the other in charge of the Institute for Research in Experimental and Applied Botany.

Thus in the case of the Arnold Arboretum, the largest and most complex of the nine separately endowed institutions concerned, all of its inside activities, such as the herbarium, library, and certain types of laboratory work, will fall under the purview of one chairman, while all matters appertaining to the maintenance of its grounds and plantings, and those phases of research that deal with the living plants, will fall under another chairman; and its general policies, research, publications, and teaching program will be developed and supervised by the chairmen and the Council. An executive officer will be designated to handle normal current affairs of the institution. This is indeed a very radical change.

Furthermore, the approved plan involves the construction of a major building in Cambridge designed to house all of the library and herbarium activities of the Gray Herbarium, the Farlow Herbarium, and the Arnold Arboretum, which means within the course of a few years the transfer of practically all of the inside staff of the Arboretum to Cambridge, and a corresponding reduction in the amount of work now prosecuted in Jamaica Plain. This move will clearly very greatly simplify what is a very complex situation, greatly reduce duplication and even triplication of effort and expense in certain fields, and will make the unique library-herbarium facili-

* On July 15, 1946, my resignation was accepted effective July 31, 1946.

ties of Harvard University much more accessible to all staff members and to graduate students than is now the case with three geographically separated units in the same general field. This matter has been discussed in previous reports. It will, however, very greatly reduce the Arnold Arboretum operations in Jamaica Plain, for there, in the future, will be prosecuted only those phases of its activities that appertain to living plants. These activities may, of course, be amplified in the course of time.

In my term of service as Director of the Arnold Arboretum since the latter part of 1935, an attempt has been made to maintain and to increase its prestige, not only as a local institution catering to the general public, but also as a national and international one in the research and publication fields. As funds became available there was no hesitation in amplifying its field of operations both at home and abroad. Thus its field work in China was greatly extended, and activities were initiated in India, Indo-China, Burma, Siam, Malay Peninsula, Philippines, Java, other parts of the Malayan region, Papuasia, Australia, New Caledonia, various parts of Mexico, Central America, South America, the West Indies, and even parts of Africa. In selecting areas outside of China, careful attention was given to those regions from which it was clearly evident that the institutional reference collections should be increased. These extensive operations were for the most part financed by grants made to competent and dependable residents of the regions involved, and the results have been outstandingly successful. Field work on the part of staff members of the institution has been financed from regular institutional funds, or through special grants secured from this or that foundation, in Canada, various parts of the United States, Mexico, Central America, and the West Indies. Thus in a decade the herbarium has been increased, in part by exchange of duplicates, in part through actual purchase of material, but largely through its own field efforts by more than 220,000 mounted sheets. Very extensive exchange credits have been established with botanical institutions in all parts of the world through the actual distribution of sets of duplicate specimens acquired through these various field operations. Within Harvard University, because of the vast accessions of material received through its sponsored field work, in excess of 130,000 specimens have been transferred to: the Gray Herbarium (123,000), Farlow Herbarium (2,470), and the Ames Orchid Herbarium, Botanical Museum (4,800), while in excess of 6,400 illustrations of plants with accompanying descriptions have been transferred to the three units mentioned. All of this was from currently received material outside of the field covered by the Arboretum, namely herbaceous plants, ferns and cellular cryptograms.

Efforts were made also to increase the already extraordinary library holdings of the institution, and by certain staff additions, more extensively to utilize the vast amount of published data therein available. Furthermore, the publication field was amplified, the technical Journal increased in size, and various and sometimes very extensive special publications were sponsored, even when it became necessary to seek financial aid outside of

the regular budgetary income of the institution. Two of the older serial titles were dropped in favor of shorter and more concise ones in Arnoldia, to replace the Bulletin of Popular Information, and Sargentia, to replace the Contributions from the Arnold Arboretum; the new names, incidentally, commemorate James Arnold (1781–1868), whose initial modest bequest made the establishment of the institution possible, and Charles Sprague Sargent (1841–1927), who actually developed it and initiated its policies on a broad base.

In maintaining the Arnold Arboretum, as to its grounds and plantings, Harvard University is most efficiently serving the public of the Boston Metropolitan area. This is proved by the enormous number of casual visitors that inspect its grounds and plantings each year. While we do not have even an approximation of the total number of annual visitors, close estimates made on certain days in the spring flowering season, from late April to early June, indicate that on occasion there may be in excess of 50,000 visitors in a single day. This is free service to the public and incidentally a very greatly appreciated service. This is, however, but a part of its local service, for as an institution it operates as a free source of information to the interested public on matters associated with plants, plant problems, and plant names. In addition to this local service a continuous effort has been made to make the institution not only more and more a national one, but also more and more international as well, in line with the general policies of Harvard University.

From a national standpoint the Arboretum not only attracts visitors from all over the country, but also from foreign lands as well. Its information service extends to all parts of the country to professional horticulturists and botanists, and to amateurs. For many decades it has served the extensive nursery interests of this and of foreign countries as well, by making available living plants, cuttings, and seeds from its more striking or interesting introductions. Throughout its history it has maintained a very high place among botanical institutions both at home and abroad, in financing its own exploring expeditions to various parts of the world with a view to introducing into cultivation new plants of potential economic or horticultural interest; and in this field it has been outstandingly successful. It has been one of our objectives during the past decade to maintain and to increase this service.

From an international standpoint the position of the Arboretum has always been clear. It has greatly increased the store of cultivated woody plants in Europe and in Great Britain, as it has within the United States. It has coöperated with foreign institutions very fully in the interchange of reference material, living plants, seeds, publications, and general information. In the past decade many of these activities have been increased, some rather radically. At the same time it has played its part in the training of graduate students, both citizens of the United States and of foreign countries, who have elected to major in this or that field covered by the Arboretum.

The material resources of the institution have been very considerably increased in the past decade. This applies not only to its library holdings and its collections of reference material, photographs, and records, but also to the financial field as well. Its chief source of support is the income from its own restricted endowment, and in the past decade this endowment has been increased by approximately $321,500.00, in spite of the 10% write-down of its capital in 1936 to offset the 10% write-up in 1930. As a matter of record the actual additions to capital received in the year just closed approximate $365,000.00, with considerable additions to be received in the coming year under the provisions of certain wills now in probate. In addition to this increase in its endowment funds, a total of about $112,000.00 has been received within the decade in the form of gifts for immediate expenditure, mostly unrestricted, but in some cases restricted, to use for such purposes as fellowships, scholarships, special travel, exploration, or publication. This amount does not include certain special grants, the total a distinctly considerable sum, that were received from such sources as the Milton-Clark fund and various other endowments for the support of this or that research project carried on by various staff members; nor does it include special grants made to support field work, such as the two seasons operations on the Alaska Military Highway.

When one considers that the decade 1935–46 covered the last half of a long continued financial depression which actually ceased only after the most destructive war of modern times was initiated, the financial record must be considered as at least satisfactory. It was from the gifts for immediate expenditure that much of the expansion activities were financed in the past decade, for the normal income in general sufficed only to take care of obligated charges.

As this report coincides with the end of an era it has been deemed pertinent to include here the following summary of the present endowment of the Arboretum, showing how it has been built up by gifts and by bequests from the modest initial sum of $99,223.21 in 1872 to its present impressive total of $3,215,983.69.

Arnold Arboretum Endowment Funds

Arboretum Construction Gifts (balance)	$91,223.21
Arnold Arboretum (1899)	125,650.00
Arnold Arboretum Endowment (1917)	431,661.64
Arnold, James (1872)	176,945.34[a]
Billings, Robert Charles (1904)	13,500.00
Bradley, William L. (1897)	21,040.00
Burr, Lucy Williams (1925)	47,051.78
Bussey Fund for the Arboretum (1903)	2,308.06

[a] The initial fund in 1872 was $99,335.48, but under the terms of indenture 5% of the income is added to capital each year.

Case, James Brown (1942)	50,000.00[b]
Case, Laura Lucretia (1925)	24,999.96
Case, Marian Roby (1945–46)	365,137.09[b]
Collamore, Helen (1916)	2,525.00
Cowell, Helen E. (1932)	50,000.00
Cowell, Mr. & Mrs. Henry (1932)	50,000.00
Crocker, Annie Bliss (1930)	5,000.00
Edwards, Grace M. (1939)	25,355.56
Estabrook, Arthur F. (1923)	5,000.00
Estabrook, Ida F. (1925)	5,285.00
Evans, Maria Antoinette (1919)	22,240.76
Hutchinson, C. L. (1932)	29,518.60
Jewett, James R. (1940)	5,000.00
Judd, William H. (1946)	2,832.50
Loring, William Caleb (1930)	25,000.00
Mass. Soc. Promoting Agriculture (1911)	13,375.00
Phillips, Anna T. (1925)	5,000.00
Pratt, Harriet B.	5,000.00
Richards, Anna M. (1931)	423,057.22
Sargent, Charles Sprague (1928)	21,613.47[c]
Sargent, Charles Sprague (1928)	20,083.17
Sargent, Charles Sprague Memorial (1926)	1,048,489.26
Sargent, Mary Robeson (1919)	8,309.37
Shaw, Isabella P. (1925)	8,644.55
Skinner, Francis (1906)	20,000.00
Skinner, Francis, Jr. (1915)	10,000.00
Thayer, Bayard and Ruth S. (1911)	25,042.75
Weld, Stephen M. (1917)	25,000.00
Whitney, Edward (1912)	2,881.97
Williams, Adelia C. (1927)	1,000.00
TOTAL	$3,215,983.69

[b] Does not include the value of extensive real estate holdings in Weston.

[c] The original fund was $10,000.00, income to be added to capital for 100 years before any part of it can be used.

One may legitimately express the hope that the institution will continue to expand within its field, and that it may increase its contributions to the enjoyment of the public, to education, to research, to the services of amateur and professional horticulturists, locally and all over the country, to professional botanists, to its sister institutions everywhere, and to plant science in general within the fields that it covers, and thus justify its continuance and support. Too often in the case of biological institutions, more particularly those within the botanical garden area, when expansion ceases, stagnation or decline sets in.

Were I asked to indicate what I consider to be the greatest immediate need of the institution at this, the close of the seventy-fourth year of its existence, my response would be a restricted publication fund; i.e., one the income of which would be restricted for use in financing the cost of publishing popular and technical information within the arboretum field. Too often when necessary retrenchments in institutional budgets are made the publication funds are among the very first items to be reduced, or even eliminated, such funds apparently being looked upon more in the nature of a luxury than as a necessity. It is rather curious to note that for the support of research, provided one has a legitimate project, one may literally approach dozens of sources of funds and actually receive grants — frequently very generous ones — to support research; but not a cent, usually, for publication expenses. Unless the results of research be published they do not, in general, become widely available. The initial capital of such a fund need not be large, for it would be possible judiciously to increase it over a term of years by adding to capital annually the receipts from sales of subsidized publications. Here it is pertinent to remark that for a high percentage of research publications subsidization is essential to publication, for the demand for much of the output comes not from individuals so much as it does from institutional libraries. Thus the sales field is limited. In plant science the actual value of a research paper cannot be gauged by the number of copies sold. I merely observe here that the Arnold Arboretum needs no further publicity; but the knowledge of its activities in the world at large — and it is one of the most widely and most favorably known units of Harvard University — comes very largely from its widely distributed official technical and popular publications.

In 1947 the Arnold Arboretum will attain the age of 75 years. It has been my pleasure, privilege, and honor to direct its activities over the past decade, ten years charged with many difficulties due to a variety of causes, including the most destructive hurricane ever experienced locally since 1620, two recent winters with unusually heavy ice damage, an unusually large number of destructive grass fires in abnormally dry seasons, financial difficulties of one type or another, the extraordinary restrictions of the war years, with the concomitant labor shortages, radically increased cost of labor, and difficulties in relation to supplies and equipment. While I shall have no administrative responsibilities on the occasion of the institution attaining its 75th anniversary, it can only be assumed that continued success will be in store for what is, in its field, the pioneer institution, for it is actually the oldest Arboretum in the world. It is also the outstanding institution of its kind and the progenitor of between fifty and sixty arboreta in the United States alone. Some of these are small and largely built on hope and enthusiasm, but others are large and well-endowed. Thus it is that from its modest beginnings in 1872 with an initial endowment of slightly less than $100,000.00 the Arnold Arboretum has developed into an outstanding cultural, educational, and research institution as its material resources have increased; for its modest initial endowment has been

increased by gifts and by bequests by more than thirty fold to the impressive total of $3,215,983.69, to be further increased within the coming year by additional impressive sums.

1945 — 1946

Financial. — Normally the institution has been operated within the limits of its annual income, but in certain years, especially during the war when the labor staff was at low ebb and we could not purchase desired equipment, the departmental balance was fortunately increased. In 1935 this balance was $16,058.19, and at the end of 1945 it had been increased to $40,507.06. The year just closed was exceptional in that the actual overdraft or deficit was $12,108.29, which was charged to this reasonably ample departmental balance. Authorization was granted in advance for this overdraft. The causes were several, chiefly two blanket increases in labor rates, and a ten percent increase in all salaries for individuals receiving $3,000.00 or less per year, and for which no budgetary provisions had been made in advance. The badly depleted labor staff was increased, this being imperative because of the deplorable condition of many of the plantings due to lack of care in the war years. There was, of course, an increased cost for supplies and equipment, and further an unavoidable delay in the settlement of the Marian Roby Case estate. Thus it was that the maintenance costs of the Weston real estate that came to the Arboretum as a part of her bequest, assumed April 1, 1945, had to be continued as a charge against the regular Arboretum income for the year 1945–46. With the payment of a large part of the Case bequest in June, 1946, this matter is now adjusting itself.

The endowment funds of the institution were increased during the past year by a total of $365,137.09, very largely from the Marian Roby Case bequest. Toward the end of the year the modest William H. Judd Memorial Fund was established through certain voluntary gifts, now amounting to $2,833.50. Additions to capital under the terms of gift of two items amounted to $1,253.72. Still to be received is the final balance of the Marian Roby Case bequest and all of the Katherine Balch bequest mentioned last year.

In addition to income from endowment and from miscellaneous sources on which the actual budget is based, the extra-budgetary Cultural Purposes Fund was increased by $5,704.00 from 172 individuals, and the special Publication Fund was further increased by gifts from 33 individuals in the amount of $5,275.00, this fund now being apparently sufficient for the immediate publication needs of the institution. One grant of $600.00 was received from the Penrose Fund, American Philosophical Society, for use in support of a bibliographic research project. Two grants have been made to support Dr. A. C. Smith's projected botanical exploration of Fiji, from the Guggenheim Foundation and from the Penrose Fund of the American Philosophical Society. The total of all gifts for immediate expenditures was $15,679.00.

Staff. — There have been few staff changes. The institution suffered a very severe loss, on May 23, in the sudden and unexpected death of William H. Judd, for 33 years a member of its staff. Mr. Judd was in charge of plant propagation, and of the accessions and distribution records. He was a veritable one-man bureau of information on plants, plant problems and plant names, being actually one of those irreplaceable persons. See Arnoldia 6: 25–28, *portr.* 1946. Dr. H. M. Raup was promoted from an Assistant to an Associate Professorship, and under the reorganization plan he has been designated as Director of the Harvard Forest. Dr. C. E. Kobuski, after three years in the military service, reported for duty in August, 1945. In May, through arrangements made by the new chairmen, Mrs. Beatrix Farrand was added to the staff, on a retainer basis, as Consulting Landscape Gardener. The other changes have chiefly been in the labor field, where significant and very badly needed addition to the labor staff has been made.

Instruction. — The graduate student situation remained about as it was during the war years. With the close of the war the number of inquiries radically increased. The present prospects are for a distinctly increased number of graduate students in 1946–47 who wish to specialize in the general field covered by the Arboretum. The Bailey report, briefly mentioned last year, was finished and submitted during the year. It was officially approved by action of the Corporation March 1, 1946, and as the new plan goes into effect it will apparently have far reaching effects on the future program of the Arnold Arboretum, and particularly in reference to the relationship of its staff members to Harvard University through the Division of Biology. In general it should greatly strengthen the advanced instruction in botany through a closer association of staff members of the separately endowed units, of which the Arnold Arboretum is one of nine, with the botanical staff of the Division of Biology of Harvard University.

Buildings, grounds, and horticulture. — The normal amount of attention has been given to all buildings to maintain them in good condition, and certain work has been done on the newly acquired residences and other buildings on the Case Estate in Weston. A survey of maintenance costs was made during the year to see if certain savings might not be made were all building repair services turned over to the Maintenance Department of Harvard University. However, the estimates submitted showed an increased cost of several thousand dollars, and so no change was made.

We are indebted to a group of lady members of the Board of Overseers Committee to Visit the Arnold Arboretum, all personal friends of the first director of the institution, for their initiative in having prepared a special memorial to Dr. Sargent. This took the form of a beautifully designed and executed bronze plaque, 30 by 21½ inches, which was installed May 12,

1946, on the right hand pillar of the Jamaica Plain gate. The inscription reads:

CHARLES SPRAGUE SARGENT
1841–1927
ARNOLD PROFESSOR OF BOTANY
IN HARVARD UNIVERSITY

FIRST DIRECTOR OF
THE ARNOLD ARBORETUM
1872–1927
THE ARNOLD ARBORETUM, HIS CREATION,
IS A LIVING AND ENDURING MEMORIAL

We are under very special obligations to Mr. William P. Long, Chairman of the Boston Park Department, for his continued interest in the Arboretum and its problems, as evidenced by the entire renovation of the road surfaces in May by the Park Department. Very extensive repairs were made as needed and the entire road, except that in the Peters Hill section, was re-tarred.

The attractiveness of the grounds decreased during the war years due to circumstances beyond our control, chiefly labor shortages and our inability to acquire needed equipment. Some of the plantings actually approached a deplorable condition. There has been some criticism of the conditions of the plantings, but this has come largely from individuals who maintain no estates and who hence were not in a position to judge fairly. Estate owners, subject to perhaps even greater restrictions than was the Arboretum during the war years, very generally understood the situation.

Following the close of the war this matter was critically considered. Two staff members returned to service following their honorable discharge from the Army, Mr. Heman Howard as Assistant Horticulturist and Mr. Alfred Fordham as Assistant Propagator. We were fortunate in securing the services of a well trained and skilled tree specialist who has the pruning program well under control. Because of the really vast amount of work that needs to be done, it is estimated that it will take him a year or two to go over all of the plantings. In the meantime, however, special attention is being given to those trees that are most conspicuous or in most need of attention, the results of his work being already evident. In any event the trees and shrubs are now receiving the care that could not be extended to them during the war years. Three ex-service men have been added to the labor force, bringing its total up to fourteen. The services of four high-school boys were secured for the summer months. With this additional labor we can, even within the present open season, go far in repairing the ravages due to neglect of plantings, damage by snow and ice, and that by storm and fire. As a simple example, over fifty truck loads of dead or

superfluous stems and branches were removed from the lilac collection alone, and several other collections have been dealt with proportionally.

We have acquired certain new equipment, this being necessary to keep labor costs within bounds. Included are two sickle-knife mowers for use in those areas where the tractor cannot be utilized to advantage. The most useful item is a Worthington "Grass Blitzer" mower, the five reel type. Its use in the extensive linden, maple, elm, and beech areas eliminates all work of raking and hauling hay. The areas are maintained in much more presentable condition, and the grass clippings left on the ground materially benefit the soil. The Ford-Ferguson tractor has increasingly proved its worth, being in almost continuous use. The radically increased cost of labor forces us not only to become more and more mechanized, but also to keep the machines working continually. We are constantly looking for specialized machines, by the use of which hand labor can be eliminated, for it is only by the utilization of such labor-saving devices that we can hope to cover the amount of work that must or should be done and at the same time keep within the budget allotment. An outstanding example of reduced labor costs is that shown by the maintenance of the shrub collection. This large tract was formerly cultivated entirely by hand. With a judicious rearrangement of the beds, elimination of alternate grass walks, and other improvements permitting the use of mechanical equipment and weed killers, most of the hand work has been eliminated and the actual cost of maintenance reduced to about one-fifth of what it was before the new system was installed. In conjunction with labor costs Mr. Williams has installed a simple daily record, so that we can now determine the exact number of man-days and boy-days involved for thirty-five different classifications.

On the Case Estates in Weston, a considerable amount of work was required in eliminating certain plantings, thinning of others, and general work in cleaning up of certain buildings, with essential repairs as necessary. The nursery space was enlarged and some large seed beds established. Several thousand cuttings were rooted in connection with certain projected horticultural investigations. The large fields were again cover cropped, in preparation for planting in the spring of 1947. At times when the necessary work at Weston is under control the men report at the Arboretum for work on its grounds.

The town of Weston, seeking a site for a new elementary school, studied three possible tracts, two of them on land already owned by the Arboretum and another on adjacent land. Since it seemed possible that the more desirable tract, from our standpoint, might be taken under the right of eminent domain, the University offered about forty-one acres, including the buildings thereon, to the town for the very modest sum of $10,000.00. This was from the Louisa W. Case gift of 1942, and the arrangement was made with her full knowledge and consent. As this was practically a gift to the town of Weston, the local authorities were greatly pleased, and this augurs well for our future relationships in Weston with the local residents and town officials.

Through an agreement made with the Department of Landscape Architecture, Graduate School of Design, Harvard University, that unit has been granted the use of several acres on the Marion Robey Case estate for the possible development of demonstration plantings. The Arnold Arboretum is free of any financial obligation in reference to this project. The use of the land, which is not adapted to anything we may wish to do in Weston on behalf of the Arboretum, was granted to the Landscape Architecture Department as a courtesy.

It became necessary to remove the remaining material in the nursery adjacent to the State Serum Laboratory building in the spring. Some of the plants not needed for Arboretum purposes were presented to the University and to Radcliffe College. The valuable plants needed by the Arboretum were moved to Weston and planted in a special nursery there. The large nursery on South Street will be continued for another year, after which some of the plants will be placed in the collections and others will be transferred to Weston.

During the year 59 living plants, 72 lots of cuttings and scions, and 25 packages of seeds were received from various sources in the United States and a few packages of seeds from foreign countries. To various institutions and individuals in the United States and Canada 261 living plants were distributed as well as 163 lots of cuttings and scions and 60 packages of seeds, and a few packages of seeds were sent to institutions abroad.

With the close of the war, interest in the Arboretum has become evident in the greatly increased number of visitors. Very many of these have the interest of the institution at heart and their very presence assists materially in protecting the place against vandalism on the part of irresponsible boys. On May 15 the institution was honored by acting as host to more than five hundred delegates to the National Convention of the Garden Club of America, this large group being escorted through the grounds by staff members of the institution. Arrangements have been completed to stage certain important demonstrations in the Arboretum for the meeting of the National Arborists Association in the late summer.

Perhaps as one result of reductions of controls during the war years, it is becoming increasingly evident that vandalism in the Arboretum is approaching an all-time high. One evidence of this is the extraordinary number of grass fires during the drier parts of the spring and fall seasons. In one recent season we experienced more than seventy fires, more than half of which were so serious that the fire department services were required. During the last year when the spring and fall seasons were fortunately not so dry, there were about forty fires. These are obviously set by boys. Since the Arboretum is open to the public from sunrise to sunset every day in the year, these young vandals cannot be excluded; neither can the Arboretum maintain guards at all times, before and after working hours, Sundays and holidays.

However, when the weather is such that the fire menace is acute, practically the entire maintenance force is distributed to strategic points and

assigned the task of watching all groups of boys. When holidays and after office hours are involved this increases our labor costs, as we must pay the men one-half more per hour than the regular scale. Naturally time devoted to watching for fires distinctly reduces the labor efficiency, for while so assigned the men can do little or no regular work. Police protection has been meager during the war years for the simple reason that the Police Department has been undermanned and overworked. Courteous treatment is always extended to the Arboretum by members of both the Police and the Fire Departments; and yet these constantly recurring fires constitute a distinct burden of expense on the Boston Fire Department. We have attempted to reduce the fire hazards as far as this could be done with our limited force. In the Peters Hill area strips were plowed and harrowed to form fire lanes, thus materially reducing the number of fires there and limiting their extent.

Two years ago the greater part of our magnificent collection of dwarf evergreens was destroyed by fire, and what remains is in a precarious position. Last year saw the destruction of a fine collection of Chinese firs near South Street; this past season our juniper collection was seriously damaged — and so it goes. What the institution needs and needs very badly is a uniformed guard supplied with proper transportation who shall be on duty at those times when the fire menace is great. Possibly satisfactory arrangements could be made with the Police Department, whereby the Department would be reimbursed on a per diem basis to cover services rendered. The situation is indeed a most serious one.

My personal opinion is that we should plan to protect what we have before we further expand staff activities by the creation of new positions in this or that field; and certainly a guard can be provided for from the additional income that will become available when certain bequests are paid in. We must keep in mind that the development of open spaces with closely cut grass attracts the baseball players among the youth in the spring and summer, the football players in the fall, and the amateur golf players at all seasons; and when a strip is opened down a slope this becomes an attraction for coasting and skiing in the winter. True it is that such activities are prohibited within its grounds, but the prohibition is not now and cannot be enforced without a properly authorized guard.

The appointment of Mrs. Beatrix Farrand as Consulting Landscape Gardener consummated in May should materially assist in the solution of certain outside problems. Her objective will be to initiate plans that will bring the living collections of the Arboretum to the highest possible degree of usefulness and attractiveness to the general public. Mrs. Farrand, once a student under Charles Sprague Sargent at the Arboretum, has been Consulting Landscape Gardener to Princeton University, Yale University, Dumbarton Oaks, and other important institutions in the country.

Plant Breeding. — Many of the ornamental apple hybrids bloomed last

spring and the better types have been selected for propagation. The new varieties are budded on *Malus toringoides* root stocks and are grown to flowering age before final selections are made. Consequently about ten years must elapse before final selections are made and the new varieties are released to growers.

Several promising new varieties of cherries, forsythias, and lilacs flowered for the first time. One of the most spectacular new hybrids is a dwarf azalea which last winter behaved as an evergreen. The evergreen segregates of *Berberis mentorensis* have not proved to be outstanding, but a few plants have been retained for further tests. Some variation was obtained in the F_2 generation of X-rayed *Berberis Thunbergi*, but the segregates are not of much value. Hybrids of red × silver maple have been set in permanent location and are making very rapid growth.

Root stock experiments have been continued in an attempt to obtain dwarfing stocks for ornamental trees and shrubs and to determine graft relationships. As is well known, certain combinations do well the first year but graft union is incomplete, and the scion dies the second year. In the Pomoideae, however, there is considerable compatibility between certain genera. The tree lilac has been used as a root stock for the common and Persian lilac with promising results. A Chinese lilac seedling budded on *Syringa amurensis japonica* made more growth in one season than it had made in six years on its own roots. Budding or grafting of hybrid seedlings may avoid the high mortality of seedlings of certain species crosses.

A cytological study has been made of bigeneric hybrids of which *Sorbus* was one of the parents, including *Sorbaronia, Amelasorbus,* and *Sorbopyrus.* All of these hybrids show considerable cytological irregularity, although all are partially fertile. Work has been continued on the effect of temperature variations on X-ray induced chromosomal aberrations.

Wood Anatomy. — Professor Bailey and his co-workers, in continuation of their investigations of the comparative morphology of the dicotyledonous families, concentrated on an intensive investigation of the foliar morphology of *Illicium.* This work was carried on in coöperation with Dr. A. C. Smith as to the taxonomic phases of the subject. The accumulated morphological evidence indicates that this genus belongs in an independent family closely related to the Schisandraceae. It indicates no close relationships to either the Magnoliaceae (sensu stricto) or the Winteraceae. While *Illicium* as a genus is sharply characterized by a number of salient, relatively stable, diagnostic, and phylogenetically significant structures, the problem of differentiative taxonomic entities within the genus is a difficult one, the morphological boundaries between species commonly being vague and indefinite. Miss Lillian Nagle is completing a morphological study of the Monimiaceae for the doctorate, and Mr. W. Spackman, Jr., is initiating an extensive survey of the salient trends of specialization in the wood parenchyma of the dicotyledons.

The Herbarium. — The total number of specimens mounted during the year was 13,248, of which number 6,178 were herbaceous specimens subsequently transferred to the Gray Herbarium as noted below. However, we removed from among material mounted and incorporated in previous years a total of 5,755 specimens (5,740 of which were herbaceous plants and 15 of which were duplicates); as a result the actual growth of the herbarium was only 1,315 specimens. The total number of mounted specimens now in the herbarium is 631,452. In a way it is fortunate that the present rate of growth is slow, since all expansion space has been filled and further distribution of material into the collections cannot be made under existing conditions. The mounting staff spent a considerable proportion of their time mounting the photographs from the Linnaean Herbarium, mentioned elsewhere in this report, and in addition some time was devoted to repair work. A limited number of clippings and mounted illustrations was inserted into the herbarium.

Although accessions during the war years have necessarily been below normal, a greater influx of material is to be expected in the near future. Certain institutions in China and other parts of the Old World have been accumulating substantial amounts of material on behalf of the Arboretum, and shipment of this may be expected as soon as transportation conditions permit. These forthcoming acquisitions will increase the strain upon our storage facilities; at present the available space for storage of unmounted duplicates, like the herbarium, is crowded to capacity.

During the fiscal year the Arboretum received approximately 54,999 specimens, acquired in the following manner: gifts, 1,673; for identification, 2,705; subsidy, purchase, or on salary basis, 18,405; and exchange, 32,216. The largest single acquisitions were 25,533 Argentine specimens received from the Instituto Miguel Lillo, Tucumán, in exchange, and about 5,000 specimens from the same institution received on a subsidy basis. Other important collections were about 3,000 specimens collected on San José Island, Panama, by Dr. Johnston; 8,769 specimens collected in Minas Geraes, Brazil, by Dr. Louis O. Williams on behalf of the Arboretum (the material subsequently transferred to the Gray Herbarium for study and distribution); and 612 specimens received in exchange from the Naturhistoriska Riksmuseet, Stockholm. A geographical breakdown of incoming material shows the following: South and Central America, 46,463; United States and Mexico, 3,157; West Indies, 1,112; Canada, 984; Pacific Islands, 1,285; Australia, 255; Europe, Africa, and Asia, 1,061; miscellaneous (mostly cultivated), 682.

The Arboretum sent to other institutions a total of 29,558 specimens; as usual in recent years the bulk of this material was transferred to other departments of Harvard University as inter-institutional transfers, as follows: to the Gray Herbarium 23,467 specimens (17 for identification, 12,107 mounted specimens transferred, 10,588 unmounted specimens transferred, and 755 mounted illustrations transferred); to the Ames Orchid Herbarium at the Botanical Museum 439 specimens (81 for identification,

90 specimens and 268 mounted illustrations transferred); and to the Farlow Herbarium 327. To other American institutions we sent 4,453 specimens in exchange, 281 specimens for identification, and 18 specimens as gifts; to non-American institutions went 186 specimens in exchange, 380 specimens for identification, and 7 specimens as gifts. Microfilms, photostats, and publications to the value of 861 specimens were sent out on an exchange basis. The total number of specimens or their equivalent distributed by the Arboretum, therefore, was 30,419.

To 18 institutions (14 American and four foreign) the Arboretum made 33 loans totalling 1,301 specimens; members of our own staff received 49 loans from 17 institutions (11 American and six foreign), totalling 2,303 specimens.

To the catalogue of references to new species and other important literature pertaining to woody plants 2,511 cards were added, bringing the total number of cards in this catalogue to 141,161. Only 28 negatives were added to the collection representing types and other critical species; this collection of negatives now totals 4,239.

In addition to carrying on the usual amount of routine work, staff-members continued their special researches. Professor Rehder brought to completion the major project which has occupied him in recent years, namely the preparation of a Bibliography of Cultivated Trees and Shrubs. This extensive work is now in press, and its appearance will be welcomed by the numerous individuals who make frequent use of Prof. Rehder's Manual of Cultivated Trees and Shrubs, of which the Bibliography will be in some respects a supplement. Dr. Smith, continuing his collaborative studies of the Ranales with Prof. Bailey and Dr. Nast, worked on the genera *Illicium, Schisandra,* and *Kadsura;* a revision of these important genera is now approaching completion. In order to make possible a projected exploration of the Fiji Islands, Dr. Smith applied for and was awarded a John Simon Guggenheim Memorial Fellowship, for use in 1947. He also received a grant from the Penrose Fund of the American Philosophical Society, for application toward the same project. Dr. Smith plans to leave in February, 1947, to spend about nine months in Fiji in continuation of his field work undertaken there in 1933–34, with the intention of obtaining sufficient material to make feasible the preparation of a modern descriptive Flora of Fiji.

Dr. I. M. Johnston continued his collaboration with the Chemical Warfare Service in relation to the San José Project. From December, 1945, to February, 1946, on army orders, he made his third trip to San José Island, Gulf of Panama. As a result of his association with this project he had exceptional opportunities for the study of tropical vegetation and for assembling reference material. In recognition of his work during the tests at San José he was awarded a citation in August, 1945, by the Chief of the Chemical Warfare Service. Much of the detailed data that he assembled regarding San José Island and its vegetation can now be published. His detailed report, the preparation of which is now well advanced, will appear in Sargentia.

Dr. H. M. Raup devoted most of his time to the completion of two papers, one published, one in press, the former being his phytogeographic consideration of the Athabaska–Great Slave Lake region, published in our Journal in 1946, and the latter his Botany of Southwestern Mackenzie, which is now in press as a number of Sargentia.

Dr. Kobuski, after an absence of three years in military service, returned to his position at the Arboretum in August; resuming his work on the family Theaceae, he is undertaking a revision of the genus *Adinandra*. Mr. Palmer completed his revision of the genus *Crataegus* in the northeastern United States and adjacent Canada, and he is continuing his investigations of the taxonomy of hybrid oaks. Dr. Allen, after completing her manuscript revising the Lauraceae of Panama for inclusion in Woodson & Schery's Flora of that country, has begun assembling material and data for a study of the South American representatives of the Lauraceae. Dr. Perry continued her studies of Papuasian plants, with special reference to the large collections of the Richard Archbold Expeditions; she also prepared for publication translations of several scientific articles originally published in Dutch (for reference to these, see the bibliography appended to this report). Dr. Croizat continued his studies of the Euphorbiaceae, particularly of tropical America, while devoting much time to identifications of cultivated material.

My own activities, in the limited time that was available because of the pressure of administrative work, have been devoted largely to bibliographic matters and to identifying and reporting on various collections from the Old World tropics. Completed and published was the consideration of the technical names of plants proposed by William Bartram (1791), and completed and presented for publication a somewhat similar treatment of the Amos Eaton names (1817–1840). Progress has been made on a similar treatment of Muhlenberg's names (1813–1819), and the long continued Rafinesque project, the Index Rafinesquianus mentioned in previous reports, approaches completion and will be finished during the coming year. My Botanical Bibliography of the Islands of the Pacific, mentioned elsewhere in this report, was completed during the year.

Bibliography. — Dr. Frans Verdoorn edited volume three of the Annales Cryptogamici et Phytopathologici, and volumes seventeen and eighteen of A New Series of Plant Science Books. Chronica Botanica was published in installments, being chiefly devoted to historical subjects. He also continued to act as advisor to the Board for the Netherlands Indies, Surinam and Curaçao in New York City, and to supervise the Central Depository Library for the Netherlands Indies, which he established in 1942. With Dr. Pieter Honig he edited *Science and Scientists in the Netherlands Indies*, which includes a detailed directory of scientists resident in the Netherlands Indies at the time of the Japanese invasion. For the Board he is now preparing a plan for an international visitors' research station to be established in the East Indies.

Much attention has been given to the basic Index Botanicorum project, about seven thousand sheets having been added to the file during the year. The services of numerous new collaborators have been secured, notably in Finland, France, the Netherlands, Sweden, and Switzerland. Much of the work has been done by Mr. Walter Baron, formerly of the Berlin Institute for the History of Medicine, with the part time assistance of several other persons. In connection with the development of this project the following files are being developed: — a collection of portraits of plant scientists; one of illustrations of botanical gardens and botanical museums; and one of autographs of plant scientists; a card catalogue index to the literature of the history of the plant sciences; and a similar index to the literature and other data on the history of botanical institutions.

For the first time since work on the Index Botanicorum project was initiated in 1942 it was possible for Dr. Verdoorn to assign to it personal funds. His present rate of expenditure is about twice the amount of the modest subsidy provided by the Arnold Arboretum.

Other important bibliographical projects include Prof. Alfred Rehder's Bibliography of Cultivated Trees and Shrubs, the printing contract having been consummated in May. It will probably take the better part of a year to see this major work through the press. The long continued work on the Index Rafinesquianus is practically finished, remaining to be completed being only the introduction, and this is well advanced. The Bartram project mentioned in last report was finished and published, while the Eaton manuscript was completed and is now being printed.

Because of expressed desires of officials of the Smithsonian Institution, work was reinitiated on a thorough revision of my Polynesian Botanical Bibliography 1773–1935, which was published in 1937, bringing it up to date and increasing the author-entries from about 2,600 to approximately 3,900. This covers the entire Pacific basin from Juan Fernandez and Hawaii to the Marianas, Caroline, and Palau Islands, and southward to New Caledonia. The revision was completed during the year and this extensive contribution is now in press as one of the official publications of the Smithsonian Institution under the title: — A Botanical Bibliography of the Islands of the Pacific.

Because of its remarkable library facilities the Arnold Arboretum has been strong in the bibliographic field, as witnessed by the Bradley Bibliography (1911–1918), the Bibliography of the Botany of Eastern Asia (1938), and its comprehensive library catalogue (1914–1923). It is fitting that extensive work in this field be accomplished here where it is possible to gain access to most of the published literature, even including numerous exceedingly rare volumes. It may be argued that such intensive work does not benefit the individual or the institution to any great degree, but this is actually a false argument. Good bibliographic work can be done in only a relatively few centers in the world, and this happens to be one of them. It should not be forgotten that the published output in the bibliographic field is very widely used by productive botanists and by

librarians all over the world, and that service rendered in this special field is very greatly appreciated elsewhere. In this sense the Arnold Arboretum is a world institution, not merely a local or national one.

Lithoprint reproductions of rare works. — Because of the very successful outcome of the lithoprint facsimile reproduction of the very rare "Sylva Telluriana" and "Autikon Botanikon" of Rafinesque in 1943, it was decided to extend this service more particularly for the benefit of the younger botanical research institutions in the United States and elsewhere. It is now practically impossible to acquire copies of certain basic works, and even when they are rarely offered the asking price is exorbitant. The newly reproduced works, all issued in 1946, are Rafinesque's "Flora Telluriana" (1836–1838), about 450 pages, "New Flora and Botany of North America" (1836–1838), about 404 pages, "Atlantic Journal" (1832–1833), 212 pages, Blume's "Catalogus," 112 pages, Gronovius' "Flora Virginica" (1739), 206 pages and its edition two (1762), 176 pages, and Walter's "Flora Caroliniana" (1788), 252 pages. The modest unit prices for these modern reproductions vary from $2.00 to $5.00, depending on the number of pages involved.

It may legitimately be pointed out that here is a field in which older institutions with very ample library facilities can be of distinct service to more recently established ones. Of one of the above titles the only known copy in all of the botanical libraries of North America is the one on the shelves of the Arnold Arboretum library; because of the nature of the work it ought to be available in the libraries of all institutions where botanical research is prosecuted. It may further be pointed out that in another case where the lithoprint reproduction can be had for the very modest price of $3.00, a dealer has recently demanded $375.00 for a copy of the rare original; and it is a curious fact that the modern reproduction is not only easier to consult, but is actually clearer than is the rare original. As another case of recent exorbitant asking prices may be cited two items, which the Arboretum fortunately already possessed, where copies were offered in 1946 at $4000.00 each; and yet one of these was offered only two or three years ago for about one-third of the price now asked. Unfortunately, with these inflated prices the items, if sold, pass into the possession of wealthy bibliophiles, and so become lost to working botanists who need access to them.

The cost of reproducing all of these lithoprint reproductions has been covered by private funds supplied by the director, but the institution receives the credit, for each bears the Arnold Arboretum imprint. There are so many rare volumes that are in relatively great demand, and the asking prices are so exorbitant that they are quite beyond the financial limitation of the average botanist, or, for that matter, the average botanical institution, that any institution that might elect to exploit this field could not only reimburse itself for the expenditures involved, but could actually make this field a source of revenue, where additional income is needed.

The Library. — Two hundred and ninety bound volumes were added to the library and 147 pamphlets were catalogued, bringing the totals to 46,131 and 13,753 respectively. Five hundred and seventy author and subject cards were filed in the main catalogue and 4,930 cards were distributed into the Gray Herbarium card index.

Inter-library loans were many and varied, the total number handled, including incoming and outgoing loans, reaching the impressive figure of 686, the number increasing year by year. Our own borrowings are very largely limited to other Harvard libraries, it being only occasionally that we have to go outside of the Boston area for a needed book. This service is one that is very greatly appreciated by staff-members of other institutions where the library facilities are much more limited than is the case here. This is another field where the institution can be of very great service to others in actual loans of needed volumes, or in having microfilm or photostat reproductions made where the high value or extreme variety of a volume renders its loan undesirable. During the year many orders for microfilm and photostat work were filled, in some cases covering entire volumes.

The large photograph collection fills a distinct need, it being much consulted by students, by nurserymen who are planning new catalogues, and by authors seeking illustrations for their about-to-be-published books.

Much time is devoted each year to scanning second-hand book catalogues. Although it is relatively rare that we thus locate a needed work that we do not have, occasionally an item well worth while is located. This year perhaps the most noteworthy case was a nearly complete set of the very rare Rafinesque "Speccio delle scienze" (1814), with, most surprisingly, its original fascicle covers. In this case we realized what we were purchasing even if the dealer did not realize what he was selling, as the price paid was a very modest one.

Much attention has been given to the matter of reinitiating our exchanges of technical publications with foreign institutions in former enemy or enemy-occupied countries. Contacts have been reinitiated so far with forty institutions in eleven countries. It is interesting to note that in each case, each institution had reserved a set of its technical publications to be sent in exchange for ours, immediately this became possible following the close of hostilities.

It is realized that we shall have difficulties in filling the *lacunae* in certain sets of technical periodicals due to the loss of reserve stocks of current issues in certain publishing centers, such as Berlin, Leipzig, Tokyo, and other cities devastated by war. Doubtless in some cases we shall have to be content with microfilm or photostat records. However, every effort will be made to complete the files in the case of essential publications.

Linnaean microfilms. — The acquisition by the Arboretum of a complete microfilm record of the Linnaean Herbarium was mentioned in previous annual reports. A complete set of 5×7 prints has now been made

from this microfilm, and these prints are filed in the Arboretum Library in two steel 5-drawer cabinets. Each print is mounted on a stiff card measuring $7\frac{1}{2}$ by $9\frac{3}{4}$ inches, occupying about half of the card. On the other half is a printed label bearing such pertinent information as the name of the plant in the Linnaean Herbarium, the number under which it is described in Mr. S. Savage's "A Catalogue of the Linnaean Herbarium" (1945), etc. There is ample room on each card for annotations pertaining to the proper modern name of the species, original place of description, references to critical discussions, etc. It is believed that the collection will be more useful maintained as a unit in the sequence of the Linnaean Herbarium than if the prints were scattered in the general herbarium. Each mounted photograph may be removed from the files for examination and comparison with specimens. Such a collection will increase in value as it is used, as annotations by competent authorities are added to the cards. The total number of entities is 14,207, but on about 462 cards there are two or even three photographs, due to the fact that certain specimens were photographed more than once to show details, important annotations, etc. The collection, therefore, contains approximately 14,669 photographs.

These prints, while scarcely sharp enough to make good half-tone reproductions, do generally supply a fairly graphic representation of what Linnaeus had before him. From a critical examination of these photographic records in association with the printed Linnaean record and in association with actual specimens collected in the various historical localities, one can generally gain a very definite idea as to what a Linnaean binomial, that was based on an actual specimen, actually applies. The Arboretum is very fortunate in having this photographic record, for here again it is now in a position to assist botanists elsewhere by loaning individual prints that may be required for examination.

Atkins Institution of the Arnold Arboretum. — With the initiation of an active campaign toward the end of the preceding year to remedy the overgrown conditions of the plantings, very excellent progress has been made and practically all signs of neglect have been removed under the vigorous campaign initiated by Mr. Walsingham. Even the coarse grass was removed from the stream-beds, which were cleaned during the dry season, as well as that in the boundary fences. The year incidentally was more favorable than the preceding one, with a much more ample and better distributed rainfall (56 inches). There were no severe storms, nor were low temperatures recorded during the winter months. Taking advantage of favorable conditions, additional plantings were made in the *Albizzia, Bauhinia, Cassia, Ficus,* and other sections, and over 300 small palms that had been grown in pots were planted in the garden.

Work was initiated in June on the regeneration of a native forested area in Belmonte. Several hundred seedlings of teak, lemon wood, and mahogany were planted, and about 500 seeds of both teak and mahogany were

planted *in situ*. If the resulting young plants withstand the dry season this interplanting will be extended next year. Eight of the new cement beds were used for sowing teak seeds, four in April and four in May. Excellent germination resulted and there may be available between two and three thousand seedlings by next year for transplanting.

Essential repairs were made to the watchman's house, and the new cement water cover on the nursery site, which had cracked at the corners, was repaired and is again in service. In the renovation program from October onward, after the planting was finished, most of the labor force was assigned to a general clean-up of the entire garden area. The results are very striking.

While, as in the preceding war years, no students were actually in residence, many more individuals visited the institution than in recent years, some spending from a week or two to as many as eight or ten weeks. Various Cuban government officials continue their interest in the institution by visiting it at intervals.

In June over 600 packages of seed were received from the New York Botanical Garden from the Mexican collections of Mr. E. J. Alexander. From other sources 82 packages were received, and 97 lots were collected from plants growing in the garden for local use. During the year the distribution comprised 323 packages of seeds, 263 living plants, and 27 lots of cuttings for propagation. It is becoming more and more evident that in the mature plants now being grown at Soledad, both native and exotic species, an exceedingly valuable asset is now actually available in Cuba for the benefit of that country.

Under the reorganization plan which has been approved and is now actually in effect the Atkins Institution has been divorced from the Arnold Arboretum, and henceforth will be known as the Atkins Garden and Research Laboratory, under the direction of Dr. Arthur G. Kevorkian, who will spend a part of each year in Cambridge and a part at Soledad.

Publications. — As usual, four numbers of the Journal were published; these included 16 papers by 12 authors, a number smaller than average because of the length of important contributions by Dr. Allen (in volume 26, numbers 3 and 4) and by Dr. Raup (in volume 27, number 1). No numbers of Sargentia were published, but one issue, containing an account of the botany of southwestern Mackenzie by Dr. Raup, is in press, and the manuscripts of one or two additional numbers are well advanced. The usual numbers of Arnoldia, our bulletin of popular information, a service that is highly considered in both professional and amateur horticultural circles, were published.

In addition to the periodical publications mentioned above, two major works by staff-members are now in press. The first of these, Prof. Rehder's Bibliography of Cultivated Trees and Shrubs, is an extensive work giving the synonymy and full bibliography of all the entities in his much consulted Manual of Cultivated Trees and Shrubs. The other is the second part

of Mrs. McKelvey's Yuccas of the United States, an extensive treatment which will complement the first part, published in 1938. The second part of this very important study will be published in the same format as the first part and will similarly be elaborately illustrated by the author's striking photographs.

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